Paws for thought: Assessing the efficacy of monitoring techniques for rare and elusive species

Elizabeth Anne Moorcroft

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I, Elizabeth Anne Moorcroft, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the work.

Abstract

Density estimation is vitally important in the conservation of endangered species. One non-invasive way of observing animals in the wild is camera trapping, a technique that has increased dramatically over the last 20 years. Models applied to the results from camera trapping can produce estimates for density. These techniques are now widespread, so it is now extremely important that the methodology is correctly and consistently used. This thesis reviews the current guidelines for camera trap capture-recapture survey design, and shows that few surveys currently meet these guidelines, thus, many density estimates published in the literature may be systematically biased. However, the guidelines themselves may not be appropriate under realistic movement conditions. A simulation model was developed using a statistically derived movement model for snow leopards, and this was used to explore the effect of survey design on the reliability of camera trap data used in Spatially Explicit Capture Recapture (SECR) analyses. I present evidence that basic assumptions about the movement patterns of the target species affect the accuracy and precision of SECR. As a result, SECR is less accurate when large survey area are used than was previously assumed. In addition, minimum capture numbers are currently used as a guide to the accuracy of density estimates. However, based on the simulation results, other measures such as distance between recaptures, and number of the individuals captured are better guides as to the accuracy of a density estimate. Finally, a possible new method for monitoring animals is introduced, a generalisation of the Random Encounter Model (REM) of density estimation. Whilst this methodology is not precise enough to study snow leopards, it opens up the possibility of applying the model to a wider range of sensors.

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Chapter 1

Introduction

Contents

Today, the world is the middle of a man-made mass extinction period (Ceballos et al., 2015). The International Union for Conservation of Nature and Natural Resources (IUCN) estimates that 26% of mammal species are threatened (IUCN, 2015) and, if the risk factors are not eliminated, they could be on the brink of disappearing forever. Man-made factors such as climate change, urban expansion and poaching, are the root cause for crisis in many of these species (Vitousek et al., 1997).

Ensuring continued biodiversity for future generations is not just a moral imperative, it also has important implications for human wellbeing, as well as financial benefits (Ceballos et al., 2015). In 1997, the value of "ecosystem services" [1] was estimated by Costanza et al. (1998) at almost twice the gross world product. However, the value that the ecosystem produces is often not fully recognised by government or industry, and therefore is not taken into account by policy makers. Unless attitudes change dramatically there maybe serious economic repercussions that effect millions of people.

[1] Ecosystem services is a catch all term including: the benefit of climate regulation, food production, and ecotourism, to name but a few.

Figure 1.1: Comfortable snow leopard cub. (Tambako, 2014). Published under Create Commons license

One of the animal families at risk from these man-made factors is the family Felidea, the cat family, a diverse, beautiful and iconic group. They live wild on five continents and form eight major lineages with 37 different species (O'Brien and Johnson, 2007), 46% of which are recorded as threatened in the IUCN Red List. They vary from the small black-footed cat (*Felis nigripes*), weighing in at an average of 1.6 kg (Skinner and Chimimba, 2005; Sunquist and Sunquist, 2002), to tigers (*Panthera tigris*), which can weigh more than 300 kg (Sunquist and Sunquist, 2002; Heptner, 1992). As well as having a wide variety of sizes, they can also have a diverse range of unique markings on their coats such as blotches, spots or stripes. These markings act as camouflage, but they also make animals individually recognisable (Karanth, 1995). Many felids are also secretive and difficult to find in the wild, and taken together these behavioural traits can cause difficultly in population estimation (Karanth, 1995; Riordan et al., 2015). Snow leopards (*Panthera uncia*, Figure 1.1) are the focus for the majority of this thesis, a large cat weighing between 35 kg and 55 kg, a body length of 1 m - 1.3 m, and a relatively long tail of between 0.8 m - 1 m (Hemmer, 1972). Snow leopards have evolved to live in mountainous and snowy terrains by having a camouflage coat of white, pale grey and yellow, with

dark grey and black rosettes and spots (Network, 2014). Recently, unprecedented large-scale GPS tracking studies have been performed on snow leopards, and this data was shared by Tom McCarthy and Örjan Johansson (McCarthy and Johansson, 2013) for the purpose of this thesis. The dataset provided by Tom and his team is one of the largest and most comprehensive telemetry datasets available to study, and provides the best available basis for the investigation in this thesis.

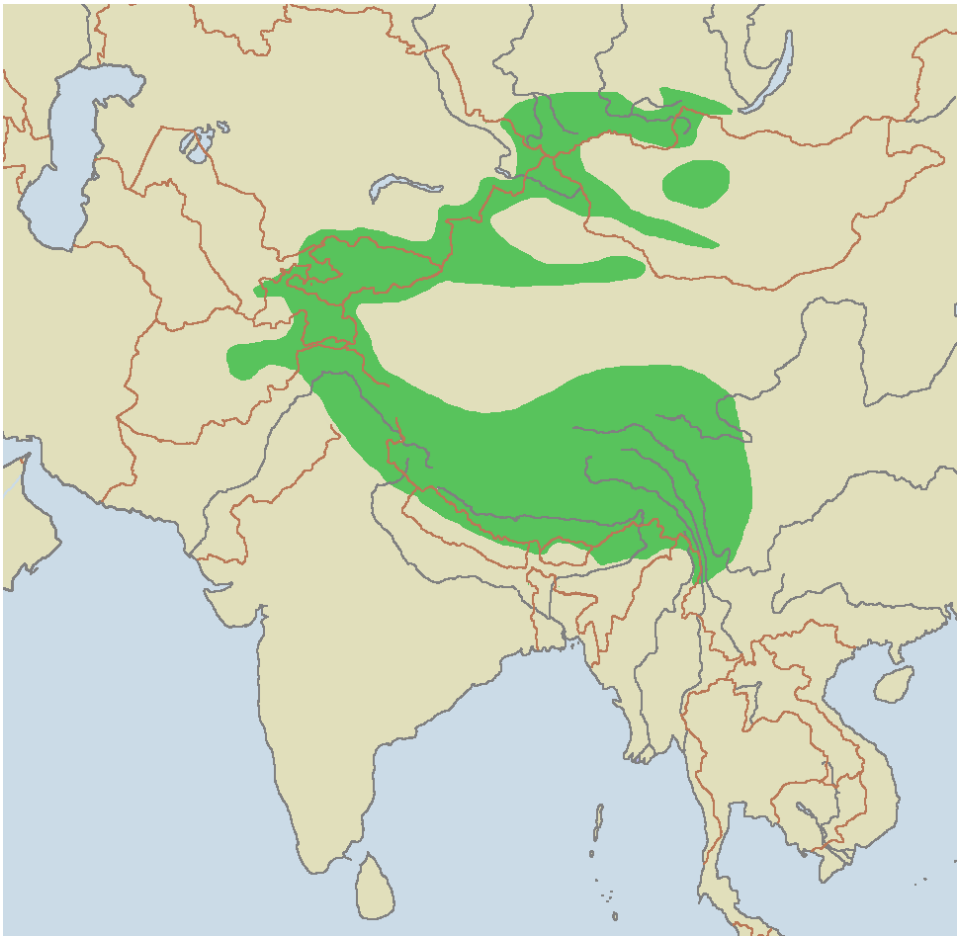


Figure 1.2: Estimated range of snow leopards. Dark green represents snow leopard territory, red lines are country boundaries, and grey lines are rives. (VIBBER, 2016). Published under GFDL

Snow leopards live across 12 different countries in central Asia in difficult to reach mountainous locations (figure 1.2); however, this widely-spread population is highly fragmented, which can reduce genetic variation and will result in increasing difficulties for snow leopards (Riordan et al., 2015). Estimates of snow leopard numbers are uncertain but, as of 2008, there are believed to be only 4000 - 6600 re-

maining (Jackson et al., 2008). Given this, the IUCN have classified snow leopards as endangered, and believe that the population is still falling (Jackson et al., 2008). There are multiple man-made factors which have caused this fall in numbers (Shehzad et al., 2012). Li and Lu (2014) showed that the there was an increase in trade in snow leopard parts in developed areas of China, with an estimated 1.2% of the snow leopard population being poached in their study region annually. Another risk factor is the reduction in natural wild prey available for snow leopards to eat. The majority of snow leopards' wild prey are large ungulates, with the occasional small mammal or bird (Anwar et al., 2011), and the numbers of these animal are under pressure. For example, wild prey, such as the Argali (*Ovis ammon*), are themselves near threatened (Harris and Reading, 2008). The reduction in wild prey is partly caused by increased foraging competition from livestock (Mishra et al., 2003, 2001), and this has led to snow leopards hunting livestock instead. There is some dispute about this, however; Oli (1994) states that snow leopards do not eat livestock because there is not enough wild prey, rather that livestock is more plentiful and easier to hunt. Whatever the underlying reason, snow leopard feeding on livestock leads to the final risk factor of retaliatory attacks from humans (Suryawanshi et al., 2013). This is an understandable reaction as the cost of livestock predation to farmers can be up to half the average income of a rural family (Bagchi and Mishra, 2006), and government schemes to offset this often do not reach sufficient levels to replace lost income and so stop retaliatory attacks on snow leopards (Mishra et al., 2003).

The snow leopard is the apex predator in its natural environment (Network, 2014), and the loss of this species would result in loss of bio-diversity and trophic downgrading (Shehzad et al., 2012; Wilman and Wilman, 2015). Therefore, it is vitally important that the snow leopard is protected, not only for its own sake, but because of the disastrous effects this may have on the local ecology and economy. There are multiple suggested stratagems to preserve snow leopard populations, including: promoting good practice for farmers so that the impact on wildlife is reduced; education for the locals in order to stop retaliatory attacks; and adequate compensation for attacks on livestock by snow leopards (McCarthy et al., 2003;

Mishra et al., 2003; Jackson et al., 2008). There have also been calls to strengthen national and international rules, including the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and their enforcement (Theile, 2003; Jackson et al., 2008). Whilst there may be multiple strategies to protect snow leopards, it is important for researchers to know whether the strategies are producing the desired results (Legg and Nagy, 2006). To do this, researchers monitor the change in the size and the dynamics of the population (Yoccoz et al., 2001; Caughley and Sinclair, 1994). The direct approach of counting all the animals in the area by hand is often impossible, and past methods of extrapolating animal numbers from visible signs of animal presence, such as pug marks or indices, have proved to be invalid (Karanth and Nichols, 1998; Gopalaswamy et al., 2015). It is important to note that there is a sizeable body of literature that warns against the excessive monitoring of animals. It has been pointed out that much of the literature produces estimates with low precision, and therefore, when comparing with past studies, it is not possible to see whether there has been any change in population size (Legg and Nagy, 2006). As a result of low precision, many studies could be a waste of time and money. One of the cause of poor quality studies has been survey design, and so in recent years, there have been repeated calls for improvement in survey design and funding (Lindenmayer and Likens, 2010; Legg and Nagy, 2006; Martin et al., 2007).

1.0.1 Monitoring cryptic species with camera traps

Camera traps are one method of monitoring that is non-invasive; therefore they can be used to monitor animal behaviour as if humans were not present. They are camouflaged camera units placed throughout a study area, which used to be triggered by movement through an infra-red beam, but are now often triggered by changes in heat. This was partly caused by infra-red beam originally being formed of two units (Rovero et al., 2013). As camera traps have become a better understood tool, combined with the advances in technology over the last 20 years, they have become more accessible to researchers and the number of publications using camera traps data has increased dramatically (Rowcliffe and Carbone, 2008).

The structure of any camera trapping study should be dependent on its purpose, the environment, species under investigation and any models that will be applied to the results. Many of these survey design variables have been identified as important indicators of having a successful capture event (Kelly and Holub, 2008; Rowcliffe et al., 2011; Negrões et al., 2010; Foster and Harmsen, 2012; Garrote et al., 2011; Guil et al., 2010; Kelly, 2008; Kays et al., 2009; Tobler et al., 2008). Despite these factors being identified as important to the capture rate, and the implications survey design has on how the data can be used subsequently, they are often poorly reported (Foster and Harmsen, 2012). All of these variables are subject to constraining factors, such as safety, cost and practicality; when the ideal survey design is significantly altered because of one of these factors, the rational behind the modified survey design should be clearly explained so not to confuse best practice.

To estimate density from the results of a camera trap study, a mathematical technique needs to be applied. For felids, the most commonly used method to evaluate abundance, and hence the density of the population, is Capture-Mark-Recapture (CMR). Whilst CMR techniques have been around since the Lincoln-Petersen index in the 1800s, they received a new boost in felid ecology when Karanth (1995) applied the CMR framework to camera trap data. Rather then physically capturing animals, this method uses a photograph to identify individuals, which can be done from pelage markings on felids, so a photograph represents a “capture”, or “recapture” event. CMR assumes that individuals are always identified correctly (Yoshizaki et al., 2009), and also that the captures are a random selection from the population, so that all animals have a chance of being captured. The closed population method is used in almost all the studies that implement CMR; the closed population method requires a constant population in the environment with no animals leaving or entering for the length of the study (Otis et al., 1978). There are a number of different models within closed population CMR that allow for different capture probabilities either through time, between individuals, after the first incidence of capture, or a combination of these. The CMR method is reducing in popularity as it can only be used to estimate the abundance of the target species. In

order to calculate the density of the target species, the effective sampling area needs to be known. Where the effective sampling area is the area over which the density is calculated, no the area covered by the monitoring system. As this is often undefined, an additional estimate of the effective sampling area needs to be made. There are a number of ways of estimating the effective sampling region, none of which are considered to consistently produce an accurate estimate (Wilson and Anderson, 1985; Efford and Fewster, 2013).

New methods may be able to overcome the limitations of the CMR technique described above. The spatially explicit capture-recapture (SECR) method (Royle et al., 2009a,b; Gardner et al., 2010a) uses the concept that individuals live in territories, or home ranges, to aid population estimation. Specifically, it assumes that more captures of an individual are likely near the centre of their home range, and that the number of captures reduces with distance to the centre in a predicable manner. The decrease in capture rate is described within the SECR by the *detection function*, and SECR allows for the detection function, and distribution of home range centres, to be chosen from multiple distributions, which allows for a better fit to the data if fully explored. The most commonly used detection function is based on two parameters, g_0 and σ. g_0 represents the probability of being captured in the centre of the home range, and σ governs the rate of the decline, such that σ can estimate the home range area. In addition, SECR has been developed in both frequentist (Borchers and Efford, 2008) and Bayesian (Royle and Young, 2008) statistical frameworks. Whilst still relatively new, this technique is quickly becoming the most frequently used density estimation technique for felid camera trap data. SECR has multiple forms including those for closed and open populations and different assumptions about the probability of capture. SECR in a closed population form has similar assumptions to the closed CMR method including: geographical and population closure, independent captures, and perfect individual recognition (Otis et al., 1978). However, unlike CMR, the capture probability in SECR does not have to be greater than zero (Sollmann et al., 2011).

SECR and CMR are well established techniques for animals with unique markings; however, many species cannot be told apart by simply examining a photograph. Rowcliffe et al. (2008) developed a method for estimating the density of species based on the number of photographs, the length of the study and the average speed of the animal. This random encounter model (REM) calculates the rate of interactions of animals and camera and, based on a random gas model in physics, which calculates the expected density of particles. The main assumption is that the animals in the survey move independently and randomly with respect to cameras. Whilst this method is not currently used for felids to any substantial degree, the simplicity of the model assumptions and accuracy of the model regardless of effort may make it suitable for difficult species because it relies of relatively few assumptions.

1.0.2 Thesis content

As discussed earlier, having an estimate of density is only of use if the estimate is unbiased, and has relatively high precision (Legg and Nagy, 2006). Otherwise it could be impossible to usefully compare densities of one location or time to another (Lindenmayer and Likens, 2010), and therefore to identify whether a conservation method is working, or how it works with respect to other methods. In order to make sure that accurate estimates of abundance or density are created, there is a large body of literature investigating whether the current methodologies are producing accurate and precise results. These have been used to create guidance for future researchers, recommend new techniques, or debunk old ones.

Many researchers have used large field studies to investigate survey design (Maffei and Noss, 2008; Wegge et al., 2004; Sharma et al., 2010). By using large surveys, it is possible to subsample to create smaller camera arrays and so compare the estimates from different numbers or placements of cameras. This methodology has several drawbacks:

- Firstly, the true density of the target species is often not known. Therefore, it is only possible to compare the density estimated with the subsampled data to the density estimated with the full camera array. There is no guarantee that

results produced by the larger array are correct and, therefore, it is hard to draw solid conclusions.

- The second problem with this method is that it cannot produce a large number of independent replicates, and it is very expensive and time consuming to produce one density estimate through field work so the cost of producing hundreds, or thousands, of density estimates through field studies would be prohibitive.

The advantage of studying density estimation techniques through field studies is that all of the complexities of animal movement including animal interactions, the movement relation to topography, and camera shyness are included in the results.

An alternative method of investigating the abundance and density estimation methods is through simulation. The number of captures expected under a given survey design can be simulated though a model, and a capture matrix created. Then the estimation technique under investigation can be applied to the simulated capture matrix, to estimate abundance or density. The advantages to this method are that the true number of animals in the simulation is known and, therefore, it is possible to compare different methodologies accurately. It is also possible to produce thousands of independent replicates quickly and cheaply. However, simulations often to do not reflect the complexity of the real system they are trying to model. To the best of my knowledge, all the published simulation studies investigating SECR and REM have used probabilistic models to generate a capture matrix (Rowcliffe et al., 2008; Tobler and Powell, 2013; Ivan et al., 2013; Efford, 2011). A probabilistic model assigns the chance of capture to cameras and the animal; in other words the capture matrix comes directly from the model. This is a limitation to these previous studies as the probabilistic model is not based on realistic patterns of movement.

The first data chapter (Chapter 2) of this thesis comprises a review of studies that reported guidelines for CRM and SECR methodologies as applied to felids, and a summary their conclusions. These guidelines are then used to evaluate the likely validity of existing felid studies.

The middle part this thesis (Chapter 3 and Chapter 4) investigates whether the guidelines that already exist (summarised in chapter 2) would produce accurate and precise results using simulations. Rather than simulate the capture matrix using a probabilistic model, in this thesis an explicit simulation of animal movement was used. This means that the capture matrix is an emergent property of the model, rather than directly modelling the pattern of captures that is expected. The second data chapter (Chapter 3) of this thesis describes the process of developing the movement model based on the data provided by McCarthy and Johansson (2013).

There is a wealth of literature studying the movement of animals as there has been a need to identify, and assess, patterns of animal movement for many decades so that researchers and conservationists can analyse habitat choices and, therefore, the impact of environmental change (Bowler and Benton, 2005). These quantified patterns are referred to as movement models and have been found in ecology literature since the 1910s (Franke et al., 2004). Simple models like stochastic differential equations (SDE), that can describe random and correlated random walks have been used to describe movement since the 1970s (Brillinger and Stewart, 1998; Brillinger, 2003). Hidden Markov models (HMM) are another form model that can be used for the study of movement. In a HMM, the movement is broken into a finite number of states that represent discrete conditions, for example travelling and resting. The states are associated with particular movement parameters, for example, resting behaviour is often associated with short movements and large turn angles (Hurford, 2009). In order to determine which is the best model for the snow leopard movement, three models were created: a continuous random walk, a discrete state model with non-Markovain transitions and a discrete state model with Markovain transitions. The continuous random walk was the simplest model used, with only two parameters for each sex; this model has the advantage of being simple. For both the discrete state models, movement was grouped into a small number of movement states. For example, vectors with small turn angles and large displacements would be grouped together, whereas vectors with a large turn angles and short displacements would be grouped elsewhere. Once the groups, or state of movement, have

been found along with their associated displacements and turn angles, the method of moving between states needs to be described. In the first case, the transitions are governed by the same probabilities regardless of the starting state and, in the second case, Markovian transitions, the probability of changing states is dependent on the current state. These two methods are both more complex than a correlated random walk, with the Markovian transitions being the most complicated. However, they are arguably a more accurate representation of the underlying system of snow leopard movement. In order to evaluate which method is the best for simulating movement a comparison had to be made on a number of different criteria. The criteria of a good movement model is that it must replicate the speed, tortuosity, and use of space that the animals exhibit. Therefore, to compare the different models, a series of metrics was developed. A set of movement data was set aside before model creation on which to test, and this was tested against simulated movements from the three models that were developed.

Once a suitable movement model was found, it was used to create movement of animals in a simulated world, in which they interacted with the cameras. In this section of the thesis (Chapter 4), multiple survey designs were compared in order to see how survey design affected the results of the SECR density estimation. The first important thing to assess was whether, in the limit, when realistic animal movement is applied, the SECR model produces unbiased estimates of density.

In the final data chapter (Chapter 5) a generalised REM (gREM) is introduced. Due to simplicity of the REM assumptions, the model can lack precision if effort is lacking; however, accuracy is normally maintained with good survey design. If CRM and SECR are not suited for snow leopard surveys due to a lack of accuracy when not enough effort is applied, then the REM may present an alternative. In addition, the extension developed here allows for the inclusion of other sensor types to be used in an REM study; for example, this method of sampling could be used with recorders to detect sounds of animal calls over longer distances. The gREM was tested under a number of different movement models to determine whether it

would be suited for use on snow leopards, and other animals at different densities and with different sensor types.

1.0.3 Impact of the thesis

The overall message of this thesis is that good survey design and effort in density estimation studies using camera traps is vitally important. Unlike the previous simulation studies that investigated animal density methodology, this thesis develops a spatially explicit movement model derived from an empirical analysis of real animal movement. This methodology resulted in different conclusions to previous studies about optimal survey design, as it shows that density estimation is more sensitive to survey design than previously thought. This is an important advance because it could have an impact on how researchers study animals in the future.

The final data chapter (Chapter 5), the introduction to the gREM model, has been published in Methods in Ecology and Evolution (Lucas et al., 2015), and provides a new methodology for difficult-to-study species. It is an exciting new development in ecology as it means that density estimates for animals that are monitored acoustically will be easier to achieve. Unlike many other density estimation techniques it is unbiased at low effort, rules governing survey design are simple, and it is easy to calculate density from the results.

Chapter 2

The tail so far: A review of survey design and density estimation as applied to felids

Contents

2.1 Introduction

2.1.1 The importance of studying felid species

One of the tools vital to conservation of any species is the estimation of their abundance and density. Having accurate and precise measures for population management is important as uncertainty can have effects on researchers understanding of the underlying ecological systems (Knape and de Valpine, 2012), which affects important conservation decisions.

Almost half of wild feline species are in danger of becoming extinct. Of the 37 species in the family felidea, the International Union for Conservation of Nature and Natural Resource (IUCN) classifies 46% as vulnerable, endangered, or, critically endangered (IUCN, 2012). However, felids can be secretive and difficult to find in the wild, and this can cause difficulty in population estimation (Karanth, 1995).

2.1.2 The evolution of data collection techniques

Over the years, different methodologies have been used to estimate numbers of animals within a specific area. Prior to Karanth's first camera trapping study of tigers

in 1995, the majority of surveys were dependent on track counting (Karanth and Nichols, 1998). Track counting methodology, when applied to wild cat populations, lacks scientific rigour (Karanth and Nichols, 1998), as it incorrectly assumes that it is possible to identify individuals by their pugmarks (Ullas Karanth, 1988; Karanth, 1995). Gopalaswamy et al. (2015) also showed, in a study based on tigers, that index-calibrated methods are often not reliable as the sampling parameters cannot be controlled. An index calibrated method generally involves using one or two smaller areas which are highly studied to infer abundance in larger less well studies areas (Gopalaswamy et al., 2015) .

Within the last 20 years, camera trapping has become one of the favoured methods of monitoring felids (Linkie et al., 2010). Camera traps are a non-invasive way of observing animals in the wild (Noss et al., 2012). The basic methodology involves placing cameras, which are triggered by movement, throughout an environment. The photographs obtained, as well as each photograph's time and location, are then used as a record of the species in the area. Camera trapping works well with those felid species that are recognisable due to pelage markings (Karanth, 1995).

Individual recognition from photographs gives researchers additional information about the target species; for example, it allows us to know whether one animal was captured many times, or many animals were captured once. This extra data can then be used to calculate a more precise result using methods such as capture-mark-recapture (CMR) or spatially explicit capture recapture (SECR). As these methods take into account the number of times an individual animal is captured it is not necessary to place cameras randomly within an environment. For example, if an animal is capture more often because there are more cameras in it's home range this can be mathematically accounted for. Therefore, cameras can be placed to maximise the number of captures. This is often desirable as capture rates for cryptic species can be low; in some environments it takes over 300 camera days to obtain a single photograph (Carbone et al., 2001).

Both CMR and SECR divide the study into equal time periods, each of these being a sampling occasion, within which the number of captures and individuals are

summarised. For CMR, the number of captures per animal per sampling occasion is summarised in the capture matrix. The capture matrix for SECR is similar but, as well as recording whether there was a capture, the capture matrix records the camera at which the capture occurred. It is possible to use maximum likelihood techniques to estimate the most likely values for parameters in both CMR and SECR.

Overall, CMR is simpler than SECR. In its basic form as laid out by Otis et al. (1978), the null model, M_0, assumes that there is an equal probability of capture, p, for each animal in the area, where there are a total of N animals that can be captured. The capture matrix provides information on which animals were caught on each sampling occasion and, based on this information, the unknown p and N can be calculated. The assumption of equal probability is unlikely because some animals have will have more cameras in their home range, or they will be inquisitive and visit more camera sites. Therefore there are a number of additional models were created that addresses some of these issues. For example the M_h model allows different capture probabilities between animals, and the M_b model adds in an assumption that the capture probability alters after an animal has been caught by the camera once. However, all these models only produce estimates of abundance whereas density is most commonly needed to compare studies. In order to convert the abundance to density, the effective sampling area (ESA) needs to be estimated. The methods of estimating the ESA are often not methodologically sound (Wilson and Anderson, 1985; Efford and Fewster, 2013), and can lead to poor estimates of density. One of the major arguments in favour of the SECR is that the estimate of ESA is carried out within the model itself. In order to calculate the ESA, the SECR estimates the centre of each animal's home range where the capture probability is g_0. Then, using a model that represents the likelihood of capture of an animal at a given distance from the centre of its home range, known as the detection function, the probability of capture for that animal at locations away from the centre of the home range is estimated. The most common detection functions are the half normal and the exponential functions. These both use a single parameter, σ, to describe how to

estimate the probability of capture reduces as distance to the centre of the home range increases.

Whilst camera trapping represents a major step forward in the field of felid conservation (Linkie et al., 2010), researchers still need to be careful that the methods are correctly applied. If data are incorrectly collected, for example if the survey area is too small, then this can lead to biases in the result (Maffei and Noss, 2008; Wegge et al., 2004). It is also important to note that different methods are founded on different assumptions, and, therefore, survey design should be based around the planned analysis because violation of the assumptions could lead to misleading results.

2.1.3 The important features of camera trap survey design

There have been numerous calls for camera trapping protocols to be consistently recorded (Meek et al., 2014; Foster and Harmsen, 2012). This would allow other researchers to replicate studies and to identify if methods are being misused.

Two of the important variables to include in survey design are: the total survey area, and inter-trap distance (Zimmermann et al., 2012). Since, in general, researchers have a fixed number of cameras to deploy, there is a trade off between these two variables. As survey area is increased, the number of individuals that are available for capture also increases; however, it also results in a lower trap density. When trap density is lower, the probability of capture for any particular animal is reduced (Karanth et al., 2011). As a result, researchers have to balance the numbers of individuals with the numbers of recaptures such that a suitable sample is collected. A suitable sample must have enough captures to calculate the parameter estimates, and fulfil the assumptions of the model. In addition, where the cameras are placed is very important. In most cases of density estimation of felids, it is important to maximise the number of captures, as a high capture probability or capture count is important in increasing precision in CMR or SECR (White, 1982; Efford et al., 2009). The survey designs can vary from one large, low density, grid to multiple small, high density, grids. Typically, large grids are run continuously for all of the

survey period, whilst small grids are run for shorter lengths of time and cameras moved between them to make up the survey period.

The total effort of the study, the cumulative time for which all cameras are deployed, is also important. The greater the total study effort, the larger the opportunities for possible captures. However, the length of the survey, is also an important factor. This is because, in the long term, animals are born, die and migrate into, and out of, a study area. Therefore, if a survey is conducted over a long time, the method of analysis should take this open population into account (Otis et al., 1978).

2.1.4 Optimizing survey design, and photographic sample, for accurate and precise density estimation

As argued above, camera trap studies should be designed on the basis of the species under consideration and the analysis that is planned, because of the different model assumptions. When researchers are designing a camera trap survey, they can only influence how many cameras are used and where they are placed but, because of funding restrictions, they are often restricted to a fixed number of cameras. A researcher has two options for controlling the capture probability: placing cameras in locations where there is a high probability of capture, or increasing the number of cameras per home range. But even with strategic camera placements there can be low capture rates, so large numbers of cameras per home range would still be needed. Wegge et al. (2004) undertook a study in an area of high tiger density, where they found that there was a systematic underestimate when the inter-trap distance was too large. A similar study was completed by Sharma et al. (2010) in Kanha, India, also with a relatively high density of tigers, which gave similar results. However, neither of these studies controlled for the number of cameras, and, therefore, they compared estimates with different amounts of effort as well as different study areas; correcting this would affect the results. There are some differences in the literature as to whether trap density or inter-trap distance is reported; however, high camera density is equivalent to a low inter-trap distance, assuming equal spacing, and whilst both terms are used in the literature, inter-trap distance will be used in this chapter. Another effect of increasing the inter-trap distance, and there-

fore reducing the number of cameras per home range, is a reduction in the number of cameras on which each animal is seen.

In the attempts to create guidelines for survey design using two methodologies:

- Many researchers have subsampled large field studies (Maffei and Noss, 2008; Wegge et al., 2004; Sharma et al., 2010). This can be a good methodology because it uses real world data, and so includes all of the complexity that can occur. However, in the majority of these studies, the true abundance and density is not known, and, therefore, the subsampled results can only be compared to the results from the larger grid rather than the objective truth. Many of these studies also do not correct for important factors, such as total effort; consequently, if a change occurs then it can be difficult to determine the cause. In addition, guidelines defined using this method are based on one species in one location and, because of this, they are not easily extrapolated to other studies.

- Other researchers have used simulations to estimate the impact of survey design (Tobler and Powell, 2013; Ivan et al., 2013; Bondrup-Nielsen, 1983; Efford and Fewster, 2013). The benefit of simulations is that the modelled factors can be explored with a likely state space, allowing sensitivity of the survey design to changes in the model factors, such as speed or home range size, to be known. As the true density of individuals in the simulation is known, it is easy to identify whether a survey design is statistically over - or under - estimating abundance or density. However, the majority of simulations create the capture matrix from a probabilistic model; this is often not based on real animal movement and does not contain the level of complexity of real world data.

2.1.5 Causes of sample heterogeneity, and solutions for dealing with it

There is natural heterogeneity within the populations that we wish to survey, caused by differences in sex, age and individuals. Individuals may have differences in

their capture probability for a number of reasons, for example differing numbers of cameras within their territory, or because they are more or less camera shy than other animals. Choosing the correct model to cope with these differences is important, as many models do not include the major sources of heterogeneity in the data. That said, some models have been developed to deal with heterogeneity in a variety of ways, perhaps the simplest of these methods being the M_h CMR model, which was designed specifically to deal with unequal capture probabilities. A probability of capture, p, is estimated for each animal that was captured (Otis et al., 1978); however, the CMR M_h model does not specify the cause of the differences in capture probability.

The SECR methodology is an addition to density estimation techniques that is becoming more widely used as it provides a more credible means of estimating density. This approach allows individuals to have different numbers of cameras in their home ranges, and, therefore, it accounts for one source of unequal capture probability between individuals by including the locations of captures in the analysis. In addition, heterogeneity also often comes from other sources such as the differences between the sexes, where one solution is to add a variable into the analysis to account for sex (Sollmann et al., 2012b; Gray and Prum, 2012). Some of the assumptions in the basic SECR do limit the reliability of results obtained from it; for example SECR assumes that home range use follows a specific pattern, and that the size and shape is the same for all individuals (Borchers and Efford, 2008). Because of such limitations, there have been many recent developments, including hierarchical SECR models. These hierarchical models, for example, may specify separate distributions for capture probabilities of male and female animals which also can be used to control for differences between subpopulations (Royle and Converse, 2014; Royle et al., 2015). Another of the other major assumptions in the classic SECR model that may not hold is the detection functions being so simple and neatly described. A number of attempts have been made in recent years to include resource use, location of home range centres (Reich and Gardner, 2014), open populations

(Gardner et al., 2010a), and unmarked populations (Sollmann et al., 2013b; Chandler et al., 2013).

There have been calls for increased reporting of how samples are formed and whether there appears to be substantial heterogeneity of capture probability between individuals, so that researchers can assess whether the methodology that has been used is correct. In a review of camera trapping methods, Foster and Harmsen (2012) recommends that each survey reports the number of individuals, the number of captures and the ratio of males to females. Harmsen et al. (2011) also recommend that capture rates of individual should be reported to give an idea as to the level of heterogeneity between individuals in the sample, as large variation in capture probabilities can still cause bias in CMR M_h models.

2.1.6 Aims of this study

In this chapter, the aim was to identify what guidelines exist for researchers using CMR and SECR. These fall into three board categories: what variables should be reported, the minimal necessary survey design, and the properties of the collected sample. After identifying the guidelines the aim of this chapter was to:

- Extrapolate guidelines to other studies, environments, and species
- For each set of guidelines, calculate the number of studies that reach the minimum standard
- Identify where guidelines are missing

2.2 Methods

2.2.1 Paper selection

To investigate camera trapping methodology used on felids, a literature review was conducted. Papers for review were selected by combining two facets of search terms: one facet for felid species and another for camera traps (Table A.1), in the search engine Web of Science (Reuters, 2012). Studies were included if they were published between 2008 and 2012 and written in English.

In order to select relevant studies, papers were discarded based on their title, and then further reduced by including studies based on the contents of their abstract, specifically: examining whether they contained an estimated density or abundance of a felid species. Non-estimation of abundance may occur because it was not the purpose of the study or because of too few captures. It may not be obvious why there was no estimation of density, therefore all papers without an abundance or density estimate were excluded.

Many papers report multiple survey areas or the same area from different times; these were included, meaning that a paper may have multiple entries in the dataset. Other papers sub-sampled their data (Di Bitetti et al., 2008; Maffei and Noss, 2008; Negroes et al., 2012) in order to evaluate different aspects of the study design. Only the full data, rather than the sub-sampled values, were included, to avoid double counting. A full list of included studies can be found in Appendix A.3.

2.2.2 Current guidelines

In this chapter, there is a discussion of the already existing guidelines for CMR and SECR for use of felids. The next subsections outline the existing guidelines in three areas of interest for field researchers:

- Variables of interest: which variables are interesting for other researchers to know about your study and how they should be reported
- Survey design, which covers aspects of the layout and handling of cameras. This contained the most existing guidelines for researchers
- Photographic sample, which covers the guidelines for how many photos should be collected and the number of recaptures

2.2.3 Variables of interest

Three main categories of variable found in the literature were collected and examined: survey design, photographic sample and estimate, and, sample heterogeneity (Table 2.1). Survey design is how the researcher chose to set up the cameras during a survey, including survey area and number of cameras. This aspect is important

as it is something that researchers have control over. The photographic sample is the results of the survey, and is important to evaluate whether enough data has been collected. Lastly, details around the sample heterogeneity were collected, as these give a better idea as to whether the choice of model was correct.

Category	Variables
Survey design	Size of the survey area (km^2)
	Inter-trap distance (km)
	Number of trap locations
	Survey effort (trap days)
	Effort per location (days)
Photographic sample & Estimate	Model type
	Capture Probability
	The number of captures
	The number of animals
	Estimated population size or density
Sample heterogeneity	The range in captures between animals
	The number of unique males compared to females
	The number of capture events for males and females
	The number of adult compared to juveniles

Table 2.1: Variables collected in the literature review

2.2.3.1 Survey design

There were three studies that were identified as producing guidelines for survey design in CMR. Maffei and Noss (2008) ran a field study on ocelots (*Leopardus pardalis*) that suggested that a survey area of less than four times the average home range would result in overestimation of density. Maffei and Noss (2008) had a large grid of cameras with a survey area up to 60 km^2, which they subsampled for various sizes of grids. The estimated home range size for ocelots in this area was 3.3 km^2, and they tested various grid sizes, including: 2 km^2, 4 km^2,12 km^2 and 60 km^2. The density estimates between 12 km^2, four times the average home range, and 60 km^2, 18 times the size of the average home range, were not statistically different; however, the smaller grids produced estimates that were much larger. Therefore, it was assumed that the 12 km^2 grid produced an unbiased estimate. However, the grids were comprised of different numbers of cameras, so it is not clear whether the result is truly related to grid size rather than trapping effort.

Both Wegge et al. (2004) and Sharma et al. (2010) chose to study the impact of inter-trap distance on the estimates of density. Wegge et al. (2004) subsampled a

grid with an area of 25 km^2 and 1 km inter-trap distance, so that there were a range of inter-trap distances: 1 km, 2.1 km and 2.5 km. The CMR methodology underestimated animal density when the inter-trap distance was 2.1 km and 2.5 km. Similarly to Wegge et al. (2004), Sharma et al. (2010) found that camera density has an impact on the density estimates when using CMR. They found 0.25 cameras km^{-2} produced an underestimation of density (an approximate inter-trap distance of 2 km). They conclude that a camera density of 0.34 cameras km^{-2}, an approximate 1.7 km spacing, was sufficient to estimate density with a coefficient of variation of between 33% and 14%. In their study area, they had an estimate of average home range equal to 41.2 km^2.

A number of simulation studies have been done on SECR methodology to calculate the optimal survey design. Tobler and Powell (2013) did a simulation study of jaguars where they simulated captures based on the SECR assumptions with jaguar movement parameters (Tobler and Powell, 2013). Tobler and Powell (2013) found that the ideal survey area may vary with animal density, for example, low density (less than 1 animals$/100km^2$) would require survey areas to be the size of multiple home range areas, but higher densities (4 animal$/100km^2$) would require only half a home range to be surveyed. They also found that camera spacing could be as large as a home range radius, allowing between two and five cameras per home range. As Tobler and Powell (2013) ran simulations to gain these results, they have a large number of replicates, and can control for multiple factors. However, the simulations they ran used the same movement model as that used in the SECR method; this was not based around real movement and, therefore, the results created may not be an accurate reflection of what would occur in real life.

SECR has been shown to be less sensitive to variation in survey design than CMR (Sollmann et al., 2012b). Sollmann et al. (2012b) ran an SECR analysis on DNA captures of black bears where they subsampled their data to compare the effect of survey area and inter-trap distance on results. This study showed that survey area needed to be at least the size of a standard home range, but not many times the size, and achieved a coefficient of variation of 13%. It also showed little difference in

estimation when trap distance was doubled. However, the capture rate in this study was much higher than as found in many felid surveys. Sollmann et al. (2012b) also had a large number of recaptures, with 393 captures from 83 individuals, and therefore impact of survey design may have more effect at different densities.

2.2.3.2 Photographic sample

Whilst researchers have no direct control over how the photographic sample is made up, it can affect the results of whichever model is used. For example, capture probability is an important variable for CMR. The capture probability, p, should be greater than 0.1 (White, 1982; Zimmermann et al., 2012) to produce a reliable estimate density. Similarly, Harmsen et al. (2011) found through a simulation study that CMR M_h measurements were biased when the capture probability was less than 0.1 and the number of individuals captured was fewer than 50. In order to obtain a reliable estimate from SECR, the most recent guideline is that at least 20 captures are required (Sollmann et al., 2012b; Efford et al., 2009), and at least 30 if covariates for sex are included (Tobler and Powell, 2013).

2.2.4 Comparison of studies to published study guidelines

The sample of papers was compared to the previously published guidelines on survey area and inter-trap distance, in order to find how many of the previous studies might be biased if these guidelines were correct. Where these guidelines are only site - or species - specific, they were extrapolated based on average home range size. Home range sizes were sourced for each site and species combination where possible and, when not possible, it was taken from other locations for the same species. The sources of home range size used in the survey area and inter-trap distance analysis can be found in the Appendix A.3.

The ideal survey area for CMR was found to be at least four times the home range area by Maffei and Noss (2008), and at least the size of the home range area for SECR (Sollmann et al., 2012b; Tobler and Powell, 2013); however, Tobler and Powell (2013) conclude that this may vary with the density of species. They suggest that this is because it increases the sample size and makes the survey area more

similar to the general area. In this chapter it was assumed that the ratio of survey area to home range size that caused overestimation was constant for all home range size. There maybe other factors that affected the ideal inter-trap distance for any particular survey but these were not considered. The sample of camera trapping papers that was collected was compared to the guidelines for ideal survey areas (Table 2.2) in order to estimate how many studies reported results that might be biased by small survey areas.

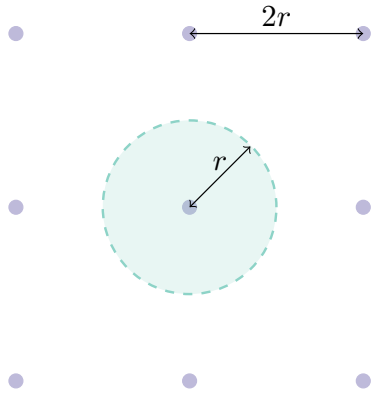
Model	Level of bias	Relative size of survey area to home range
CMR	Moderate evidence of bias	$Surveyarea < 4 \times Homerangearea$
SECR	Moderate evidence of bias	$Surveyarea < Homerangearea$

CMR = capture mark recapture; SECR = spatially explicit capture recapture

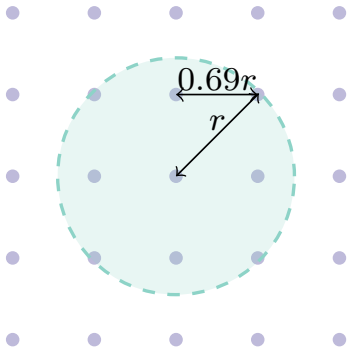
Table 2.2: Effect on estimation of density using CMR when inter-trap distance is varied relative to home range size

The guidelines in the literature for the inter-trap distance require at least one camera per home range, equivalent to one diameter spacing for CMR studies or else the assumptions are not met and the methodology is invalid. However, the results from Sharma et al. (2010) and Wegge et al. (2004) show that bias can be introduced even if there is least one camera. Both studies produced site-specific estimates for ideal inter-trap distance for tigers in areas of high density. Here, it was assumed that both sets of results would have the average home range area of 41.2 km^2 (radius of 3.61 km) that Sharma et al. (2010) reported, as this value was missing from Wegge et al. (2004). Both studies take place in areas of high tiger density. It is believed that tiger home range is affected by the density of tigers in an area, and therefore the assumption of similar average home range sizes in these two studies may be valid.

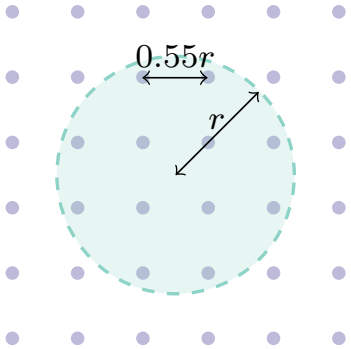
Wegge et al. (2004) found that an inter-trap distance of 2.5 km would cause underestimation of density. Therefore, assuming that the tigers had a circular home range and that there was a uniform grid of cameras, this study produced biased estimates when the inter-trap distance was more than 0.7 times the radius of the average home range. Sharma et al. (2010) found no bias when inter-trap distance was 2.0 km, but Wegge et al. (2004) found slight underestimation when the inter-trap distance 2.1 km. Based on this, it was assumed that bias is introduced at approx-



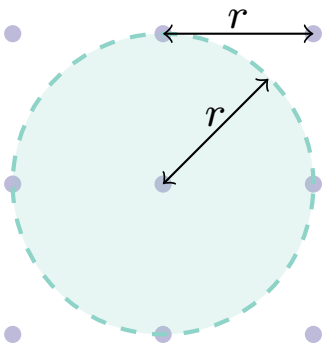
(a) Inter-trap distance = 2 home ranges



(b) Inter-trap distance = 0.69 home ranges



(c) Inter-trap distance = 0.55 home ranges



(d) Inter-trap distance = 1 home range

Figure 2.1: Optimal camera placement with a home range when inter-trap distance is equal to a) 2 home range radii, b) 0.69 of a home range radii. c) 0.55 of a home range radii and d) 1 home range radius.

imately 2.1 km, and, therefore, that 2 km was the maximum inter-trap distance for unbiased results in high density tiger studies. Assuming circular home ranges and a uniform grid, there was bias introduced if the inter-trap distance is more than 0.55 times the radius of the average home range.

There is limited information about the ideal inter-trap distance for SECR but, based on a simulation study, Tobler and Powell (2013) suggested that at least two to five cameras per home range would be needed for a good estimate of density. To guarantee a minimum of 2 cameras per home range, assuming circularity of home

range and uniform grids, the inter trap distance needs to be at least equal to the radius of the home range.

The sample of studies that were collected were then compared to these guidelines, as outlined in table 2.3, to examine how many of them, if any, fell into biased effect categories. Diagrams showing the maximum number of cameras per home range, assuming a equally spaced regular grid and circular home ranges are shown in figure 2.1.

Model	Level of bias	Maximum cameras per circular home range	Minimum inter-trap distance relative to home range radius
CMR	Strong evidence of bias	1	inter-trap distance $> 2\times$ radius
	Moderate evidence of bias	9	inter-trap distance $\geq 0.69\times$ radius
	Some evidence of bias	12	inter-trap distance $\geq 0.55\times$radius
SECR	Moderate evidence of bias	5	inter-trap distance $\geq$radius

CMR = capture mark recapture; SECR = spatially explicit capture recapture

Table 2.3: Effect on estimation of density using SECR when inter-trap distance is varied relative to home range size

2.2.5 Examining estimate reliability

If the survey design was sufficient, then the number of individuals and the capture probability, and therefore the total number of captures, that resulted should be sufficient to estimate density using the relevant technique. In CMR, the number of individuals and the overall capture probability are important for the reliability of the model. White (1982) proposed that a sample of fewer than 20 individuals could result in possible bias (Foster and Harmsen, 2012). White (1982) also suggested that $p < 0.1$ for a sampling occassion could result in possible bias, but trying to judge the reliability of the data based from the data itself can result in a circular argument (Zimmermann et al., 2012). Harmsen et al. (2011) confirmed through simulation, that if a study has fewer than 50 individuals, and $p < 0.1$, there was bias. The requirement for SECR is simpler: it requires a large number of captures - at least 20 (Sollmann et al., 2012b; Efford et al., 2009) - in order to estimate density reliability.

The proportion of the surveys in the literature sample that would have some, moderate, or strong, evidence of bias based on their sample and estimated capture

probabilities was calculated by estimating how many reached the guidelines laid out in Table 2.4.

Model	Level of bias	Condition
CMR	Some evidence of bias	$p < 0.1$
	Some evidence of bias	$n_{individuals} < 20$
	Moderate evidence of bias	$p < 0.1$ & $n_{individuals} < 50$
SECR	Moderate evidence of bias	$n_{captures} < 20$

CMR = capture mark recapture; SECR = spatially explicit capture recapture; p = probability of capture; $n_{individuals}$ = number of individuals; $n_{captures}$ = number of captures;

Table 2.4: Effect on estimation of density using SECR when inter-trap distance is varied relative to home range size

2.2.6 Estimating sample heterogeneity from reported data

Details of sample heterogeneity were collected (Table 2.1), and the percentage of the studies that included these details was calculated. Sample heterogeneity is important for assessing whether the correct model was used and, therefore, the following metrics were sought: (a) the number of individuals captured of each sex; (b) the proportion of captures of each sex; (c) the proportion in each age group; and (d) the relative capture rate between individuals.

Other researchers have commented on the unevenness of sampling, with male animals commonly being captured more than females (Sollmann et al., 2011). Ideally, this chapter would show the proportion of individuals caught in each group, for both sex and age, and compare this to the number of captures in each group. This analysis would provide evidence, if true, that current survey designs were skewing their samples towards part of the population. Large amounts of heterogeneity can cause bias in models, in even models that have specifically been designed to deal with differences in capture probability (Harmsen et al., 2011). And biased estimates caused by large amounts of heterogeneity could lead to poor inference. However, the ability to perform this analysis is limited by the amount of information recorded in the literature.

By regressing the number of female individuals against the number of male individuals it was possible to show the proportion of each sex in the sample. This was then compared to the number of male captures compared to the number of

female captures to see if the trend was replicated in the capture numbers. There was not enough information to test whether there was consistent heterogeneity in the capture probability between age groups or individuals.

2.3 Results

2.3.1 Selected felid surveys

In total, 47 papers were selected which contained 86 unique camera trap site and date combinations (Table 2.5). Out of the 13 species that were represented in the sample, four species form the bulk of the papers: tigers (*Panthera tigris*), jaguars (*Panthera onca*), pumas (*Puma concolor*) and ocelots (*Leopardus pardalis*) (Table 2.5). Papers focused on tigers represented, 13 papers, the largest group in the sample, but papers on jaguars reported the most unique survey design and date combinations. Of the seven critically endangered, or endangered, species, only four of them are represented in this sample, with the bay cat (*Pardofelis badia*), flat headed cat (*Prionailurus planiceps*), and fishing cat (*Prionailurus viverrinus*) all missing, not all of the missing species are individually recognisable and therefore might not be expected in this sample.

Species	IUCN status	No. of Papers	No. of unique surveys
Andean cat	Endangered	1	2
Cheetah	Vulnerable	1	1
European Wildcat	Least concern	1	1
Geoffroy's cat	Near Threatened	2	4
Iberian Lynx	Critically Endangered	3	8
Jaguar	Near Threatened	8	26
Leopard	Near Threatened	8	10
Ocelot	Least Concern	8	23
Pampas cat	Near threatened	2	2
Puma	Least concern	5	23
Snow Leopard	Endangered	3	5
Sunda Clouded Leopard	Vulnerable	2	3
Tiger	Endangered	13	15
Total		47	86

*Unique site and date combinations.
IUCN - International Union for Conservation of Nature and Natural Resources;

Table 2.5: Number of papers and sites per species

Design design variable	Percentage of studies which reported variables
Survey area	52.1
Mean inter-trap distance	62.0
No. of trap sites	66.9
Survey effort (total trapping days nights)	89.4
Number of days per site	44.4
All design variables	1.4

Table 2.6: Reporting of survey design variables for all species

2.3.2 Reported aspects of study design

There are large variations in the aspects of the design that are reported (Table 2.6), with only 1% of studies reporting the entirely of the survey design. The best reported were variables to do with the survey effort and the number of trap sites (Table 2.6). Variables such as average inter-trap distance and survey area are less well reported, with only slightly more than half of papers reporting these values (Table 2.6). Further details of the average survey effort can be found in appendix A.2.

CMR makes up the majority of the papers that were sampled, with CMR M_h being the most popular method. Most of the literature published at least one density estimate calculated using a CMR technique. SECR is a much newer technique and is gaining in popularity with almost half of sites giving an estimate of density calculated using this method (Table 2.7).

Method	Percentage of site species combinations using method
CMR M_0	16
CMR M_h	60
SECR	42
Other methodologies	28

CMR - Capture-mark-recapture; CMR M_0 - Capture-mark-recapture, null model; CMR M_h - Capture-mark-recapture, heterogeneity model; SECR - Spatially explicit capture-recapture

Other methodologies included CMR M_b (behavioural models), occupancy modelling, borrowed estimates of detection probability, and open capture recapture

Table 2.7: Percentage of the sites using the three main methods of density estimation

2.3.3 Survey design compared to optimised variables

The optimal survey area is based on average home range area, and is dependent on the method of density estimation used (Table 2.2). The majority of studies, 82.3%, that use CMR have moderate evidence of bias in density estimation, in one direction

or the other. However, this falls to 15.4% when SECR is used. This is because the current guidelines for achieving an optimal survey area in SECR are easier to achieve than those for CMR, and, as a consequence, fewer studies are potentially biased when SECR is used (Figure 2.2, and Figure2.3).

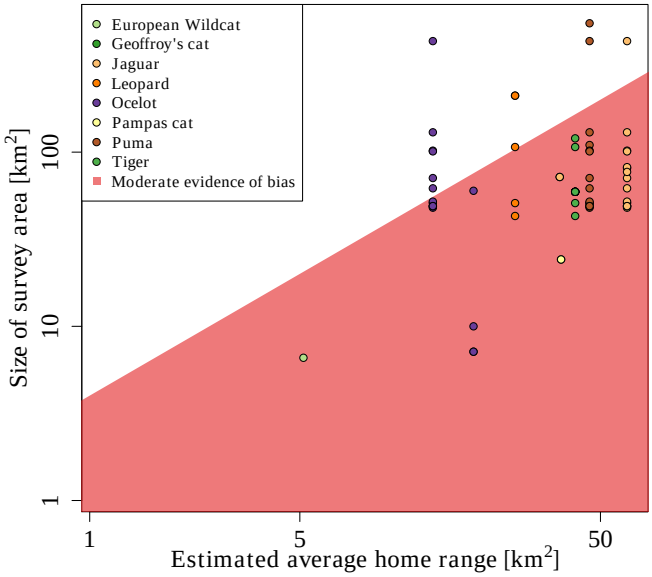


Figure 2.2: The area of survey compared to the average home range area when CMR was the method of analysis. The shaded region represents moderate evidence of bias, specified by equations in table 2.2. 82.3% of the CMR surveys were biased by this measure.

For the CMR studies, over 30% of the surveys have moderate evidence of bias, while an additional 17% have some evidence of bias (Table 2.3). Whilst none of the SECR studies show any evidence of bias due to the inter trap distance as defined by table 2.3 (Figure 2.3), it should be noted that a smaller proportion of SECR studies reported inter-trap distance: 23% compared to the 60% for CMR studies.

Altering the inter-trap distance and survey area is a measure to ensure that the capture probability, number of individuals or total numbers of captures are large enough to estimate abundance accurately. For the CMR estimates, all of the studies are at least possibly biased, as defined by table 2.4. The sample may be unrepresentative of studies as a whole as only 24% of studies reported a capture probability. However, of the studies that did, over 27% of the surveys would be biased based on

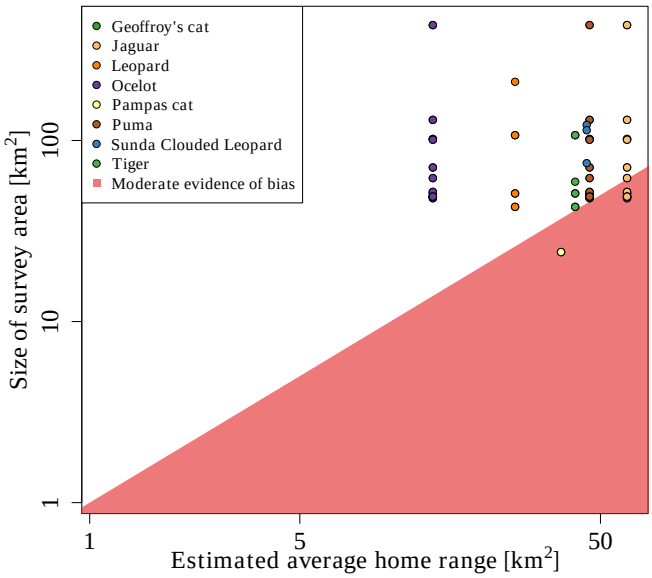


Figure 2.3: The area of survey compared to the average home range area when SECR was the method of analysis. The shaded region represents moderate evidence of bias, specified by equations in table 2.2. 15.4% of the SECR surveys were biased by this measure.

simulation results from Harmsen et al. (2011), and all the surveys would be possibly biased based on either number of individuals or capture probability from White (1982) (Figure 2.6).

The vast majority of SECR studies reached the guidelines for inter-trap distance and survey area; however, this has not resulted in all the studies gaining over 20 captures, and, therefore, many of the studies have some evidence of bias. Over one third of studies report fewer than 20 captures (Figure 2.7), which means that there is moderate evidence that their density estimates will be biased as defined by table 2.4.

The largest reported estimated density using SECR was for pampas cats, and estimated 10257 animals/100km^2 (Figure 2.7, (Caruso et al., 2012)). This is extremely unlikely as it is almost 100 times the size of the density estimate when CMR was used on the same data (11 animals/100km^2 and 18 animals/100km^2) and is almost 10,000 times the density of Pampas cats found by Gardner et al. (2010a). Based on the guidelines in table 2.4, there is only said to be evidence of moderate

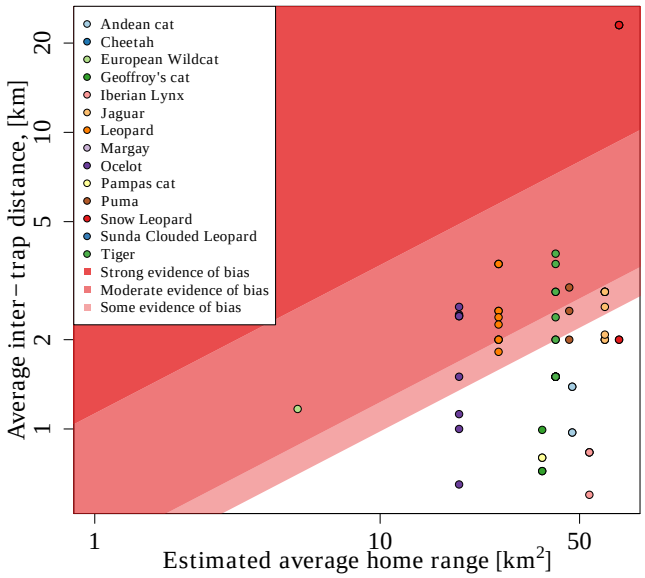


Figure 2.4: The inter trap distance compared to the average home range area when CMR was the method of analysis. 4.5%, 30.3% and 16.7% of the CMR surveys that were included showed some, moderate and strong evidence of bias respectively, as specified by equations in table 2.3. Different coloured points represent different species, and dark, medium and lightly shaded regions represents regions which studies showed some, moderate and strong evidence of bias.

bias in SECR as fewer than 20 captures are recorded. Consequently, there might be more bias created by low capture numbers then the guidelines imply. However, there are a number of other estimates that record fewer than 20 captures that produce density estimates closer to those that could be expected. Therefore, there may be some additional characteristics of photographic samples, for example number of recaptures or distribution of recaptures, that explain the extremely high density estimate made by Caruso et al. (2012).

2.3.4 Sample heterogeneity

The majority of the literature gives limited details on the results from camera trapping studies. The number of photographs, and the number of individuals in the sample, are only the only variables reported in more than half the surveys (Table 2.8). Details of the make up of the sample, the sample heterogeneity, is less well reported. Of the variables that describe the make up of the sample, the number

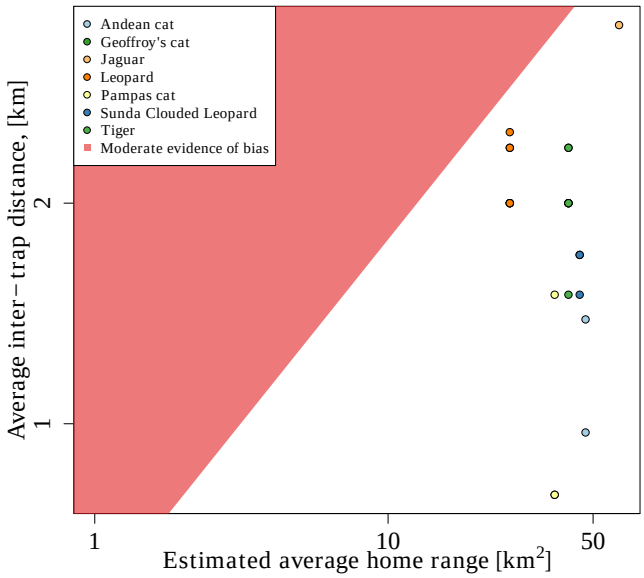


Figure 2.5: The inter trap distance compared to the average home range area when SECR was the method of analysis. None of the SECR surveys that were included were biased, as specified by equations in table 2.3, different coloured points represent different species, the shaded region represents area where there was moderate evidence of bias.

of individuals by sex is the most reported with 27% of studies reporting this variable. Other details, such as the number of captures by sex, number of captures by individuals and number of captures by age, are rarely reported (Table 2.8).

	Percentage
No. of captures	57.04
No. of individuals	89.44
No. of captures per individual	16.20
No. of individuals by sex	26.76
No. of captures by sex	5.63
No. of individuals by age	4.23
No. of captures by age	0

Table 2.8: Reporting of the camera trap results for all species

The relationship between number of males and number of females shows a trend for more females than males in the samples, as the gradient is significantly greater than 1 (Gradient = 1.54; SE= 0.12; p-value < 0.001). This relationship explains the majority of the variation in the sample (Figure 2.8), and appears to

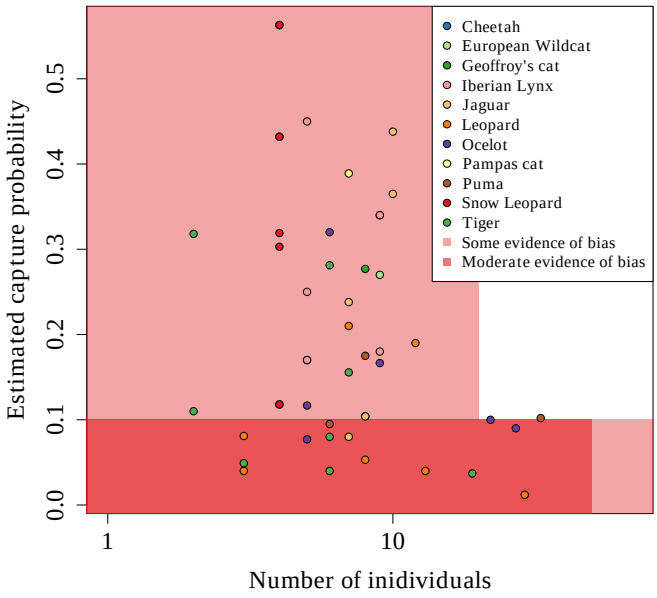


Figure 2.6: The estimated capture probability plotted against the number of individuals surveys used in CMR analyses. Showing studies that are both possibly biased, and biased, because of insufficient capture probability and individuals. The light and dark shaded region regions where there is some and moderate levels of bias, as defined by table 2.4.

be fairly consistent between species, although there is not enough power to test variation between species formally. Only 6% of the sample give the number of captures for males and females and this is too small a sample to produce a reliable regression.

The trend in the data is towards many more recaptures for males than female (Figure 2.9), regardless of there being more individual females captured in the study. Assuming that the number of individuals by sex gives a fair picture of the underlying population, this would imply that males have a consistently higher capture probability than females, and, therefore, that there is significant heterogeneity in the sample. However, there is the possibility that males have a bimodel pattern of behaviour, where they are either likely to be caught multiple times, or likely never to be seen at all. A pattern of behaviour like this would complicate any analysis attempted, in particular it might influence the reliability of any abundance or density estimate. Whilst most of the CMR studies use the M_h model, Harmsen et al.

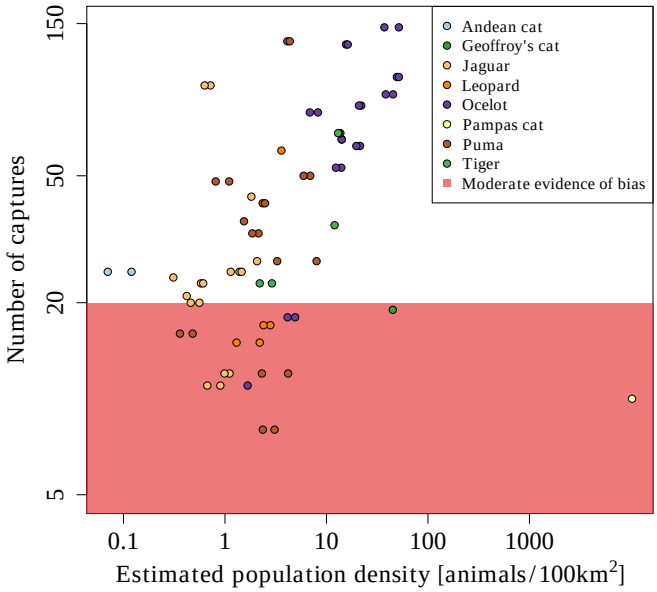


Figure 2.7: The estimated density plotted against the number of captures in surveys using the SECR analyses, showing studies that are biased because of insufficient number of captures. The shaded area represents the region with moderate evidence of bias as defined by table 2.4.

(2011) showed that extreme variation in small populations can cause this model to be less robust, and they recommend that capture matrices are published so indicate the level of heterogeneity.

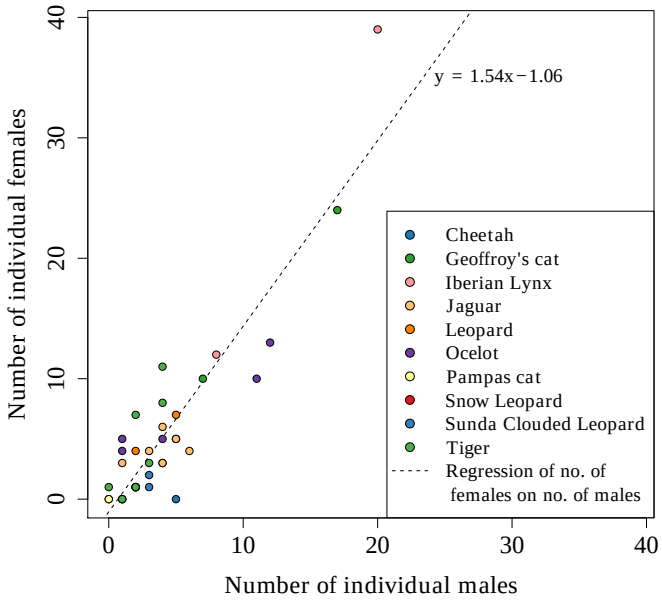


Figure 2.8: Number of individual males compared to the number of individual females. Different coloured points represent different species, and the solid line represents the linear regression of females on males.

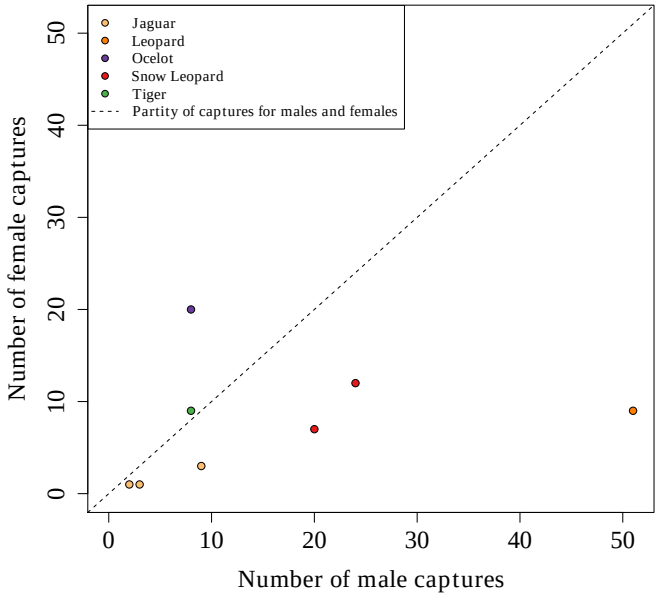


Figure 2.9: The number of male captures compared to the number of female captures. Different coloured points represent different species, and the dashed line represents equal numbers of captures.

2.4 Discussion

The aim of this chapter was to highlight variables that are already identified as important for estimating abundance or density in an accurate and precise manner, and where they are currently being under-reported in the literature. In addition, the aim of this chapter was also to identify the guidelines for survey design and photographic sample collection that already exist in the literature. Subsequently, once the guidelines were collected the aim was to see whether recent publications fall within them. The last part of the chapter tries to discover whether enough information is given about heterogeneity and, therefore, whether the choice of model can be adequately assessed using the defined criteria.

In general, few of the survey design variables or details of the photographic sample were reported in the literature, which can make it hard to determine whether the estimates of abundance or density are potentially biased, and whether the correct methodology was used. There was at least some evidence of bias in all the CMR studies that reported variables, and moderate evidence of bias in 34% of SECR estimates. If the guidelines highlighted in this chapter are correct, and they are a representative sample of all the literature, then the vast majority of studies on felids could be biased.

2.4.1 Data collection

In order for my sample to be representative of the literature as a whole, and therefore for the results of this study to be applicable, the data must have to be collected to include all possible studies. By excluding all papers without an abundance or density estimation, the sample may be biased towards studies that worked, excluding studies where the initial aim was abundance or density estimation but poor survey design caused no estimate to be reached. This is in addition to the problem of publication bias, where many results are only published if the results or data are considered interesting. Without prior knowledge of the true intended purpose, it is impossible to differentiate between studies that failed to calculate abundance or density due to poor survey design, and studies in which abundance or density was never the intended purpose.

Only one third of the wild felid species are represented in the sample, with the larger and more patterned species, which are often considered to be more charismatic, dominating. This is not a surprising result as, within conservation, it is common for some species to attract more funding and, therefore, these species are more heavily researched (Male and Bean, 2005). However, fewer than 10% of the species represent more than three quarters of the sample, and many of the existing guidelines in the literature have been created for these species.

Guidelines were often created based on the larger species with low densities; for example, inter-trap distance in CMR is based on tiger studies. The guidelines may therefore be less applicable for the smaller species, which may have higher densities and different movement characteristics. Consequently, it is difficult to make concrete inferences about whether these studies are valid.

2.4.2 Reporting of setups

Overall, there is no general consensus on what parts of the study design should be recorded or how this should be done. Individually, the variables that were selected as important for survey design (Table 2.1) were well reported; however, only 1% of the studies reported all of these variables. Poor reporting has been commented on in previous reviews of camera trapping (Foster and Harmsen, 2012), and this lack of transparency might harm future researchers as they are limited in their ability to assess the reliability of previous density estimates. Reporting the details of the survey design in a consistent manner would inform others of the robustness of their results. Only if a result is reliable can it be compared between sites and through time (Tobler and Powell, 2013), and, without the ability to compare studies, it is difficult to evaluate the relative benefits of different conservation methods, or evaluate their cost-effectiveness.

CMR was included as it is still the most common method of density estimation for the papers in this sample; however, SECR is growing in popularity and is likely to be the most-used method in future. Over 40% of the surveys in this sample, all published between 2008 and 2012, estimated density using SECR. This may be because there are many advantages to density estimation using SECR which

contribute to its growing popularity. These advantages include direct representation of density, and that, based on current guidelines, a robust estimate from SECR is easier to achieve from smaller surveys.

2.4.3 Impact of study design on density estimates

As survey design is often based on home range (Gray, 2012), current guidelines for the optimal survey area and the inter-trap distance were compared to the sample of papers. The guidelines used in CMR studies were calculated from Wegge et al. (2004) and Sharma et al. (2010) for inter-trap distance, and Maffei and Noss (2008) for the survey area. The guidelines used for both survey area and inter-trap distance used in SECR came from Sollmann et al. (2012b) and Tobler and Powell (2013). Wegge et al. (2004), Sharma et al. (2010), Maffei and Noss (2008) and Sollmann et al. (2012b) all use data subsampling to calculate their guidelines. There are some advantages to this methodology, for example including complexity of movement, topography and species interactions; however, these methods often fail to correct for extremely important factors, such as survey effort, survey area or inter-trap distance. The Tobler and Powell (2013) guidelines are based on simulations, which have the opposite set of problems and advantages; they rely on oversimplified assumptions about movement, but simulations allow for a quick extrapolation of the parameter space, so an understanding of the sensitivity of the SECR to the modelled factors can be established.

As studies often have a limited number of cameras available with which they can sample, there is a trade off between capturing many animals with a large survey area, or recapturing an animal multiple times because there is a large number of traps per home range (and therefore a smaller inter-trap distance). Therefore, when one variable is altered to avoid bias, an additional source of error can be introduced. Given a fixed number of cameras and assuming a regular grid positioning, there is a strong relationship between survey area and inter-trap distance, so they should be studied together. But when creating guidelines for surveys using CMR Wegge et al. (2004), Sharma et al. (2010) and Maffei and Noss (2008), all looked at either inter-trap distance, or survey area, without considering the effect on the other variable,

or the total effort used in the study. For example Maffei and Noss (2008) compared density estimation with a grid size of 2 km^2 made up of 6 cameras with the density estimation when the survey area was 60 km^2 made up of 26 cameras. Here, there is some difficulty in telling whether the improvement in density estimation mainly comes from the increase in survey area, or the increase in trapping effort, or equally from both. To adequately compare two grids with different numbers of cameras, it would be necessary to alter the trap effort by increasing or decreasing the number of days for where the cameras were run. For example a 2 km^2 survey area made up of 6 cameras run for 26 days could be compared to a 60 km^2 survey area made up of 26 cameras run for 6 days, as they would both have 156 days worth of effort.

Sollmann et al. (2012b) looked at the inter-trap distance and the survey area independently when creating guidelines for SECR. The methodology used by Tobler and Powell (2013), who created some of the guidelines for SECR density estimation, differed slightly. As it was a simulation study it was possible to keep the number of cameras constant and alter size of the survey area (and therefore the inter-trap distance). This is a more realistic scenario as researchers are likely to have a fixed number of cameras.

It was assumed that these guidelines would scale linearly with the size of the home range; however, there may be other factors that are involved that influence the success of a trapping design. Tobler and Powell (2013) reported that expected animal density should be taken into account when designing surveys for SECR estimation as density may affect the survey area that is needed. But other factors may also be important: for example, a more mobile species may accrue more captures than a slower species and therefore require fewer cameras per home range. Also the heterogeneity in landscape, the movement patterns and the trap shyness of the target species, and variation of these within the species may all have an effect. Alternatively, the ability of researchers to maximise capture rates may be dependent on species, or environment, and therefore certain species may require more survey effort. As there are unknown factors that may affect the optimal survey design, the guidelines that were produced may not reflect the levels of bias in the data. A good

example of where guidelines do not adequately explain the amount of possible bias is the Pampas cat study (Caruso et al., 2012), discussed earlier, where fewer than 20 captures produced an extremely large estimate of density that was classified as having moderate bias.

2.4.3.1 Survey design for capture mark recapture

In my sample, over 80% of survey areas were too small based on the results from Maffei and Noss (2008), requiring a survey to be at least the size of four home ranges. When species with smaller home ranges are being studied, this guideline is easier to reach logistically; however, for species with large ranges it may become logistically more difficult, especially in certain terrains, such as mountains or dense jungle. In the case of inter-trap distances, an effort is made to meet the assumption of at least one camera per home range, so that CMR methodology is valid (Balme et al., 2009; Reppucci et al., 2011). However, guidelines on estimating density using CMR methodology were reviewed from multiple papers, which gave a range of possible outcomes: some evidence of bias, moderate evidence of bias and strong evidence of bias. Only one study had trap spacing so large that the results may have been invalid; this study, of snow leopards, was completed by Jackson et al. (2009), and they made made an effort to achieve the one camera per home range required. However, the estimate of home range size they used when setting up the survey came from a pervious study using old techniques, from an area far from the location of the density estimation study by Jackson and Ahlborn (1989). The estimate for home range size in this thesis comes from a home range estimation study closer to the location of the density estimation study, and the home range estimate was calculated using more up-to-date techniques (McCarthy et al., 2005). This is an example of how easy it is to bias a study result despite the hard work of researchers, aiming to perform the best possible study. Large variations in animal home ranges are possible within species, and so to avoid possible biases like that which occurs in Jackson et al. (2009), it is important to have the best site-specific information about home range values. Whilst Jackson et al. (2009) was the only invalid study, there is at least some evidence of bias in 44% of studies.

Implementing both the inter-trap distance guidelines and survey area guidelines can be difficult for species with large home ranges if there is a limited number of cameras. For example, the range of an Amur tiger has been measured at 360 km^2 (Carroll and Miquelle, 2006); and this would require a survey size of at least 1440 km^2 and approximately 400 cameras to reach these guidelines. Naturally this would take large amounts of funding and manpower.

The purpose of achieving large survey areas and small inter-trap distances is to collect enough data with the correct features (capture probability and the number of individuals) to estimate density reliably. All of the CMR estimates in my sample that reported both of these variables showed at least some evidence of bias. This is unsurprising as the majority of CMR studies had insufficient survey area, or too wide an inter-trap distance, to meet current guidelines. If the vast majority of studies show some evidence of biased results when CMR is used, it is time either to phase out the methodology, or to increase the levels of survey effort applied so that results become more reliable.

2.4.3.2 Survey design for spatially explicit capture recapture

When using SECR to calculate density estimates, the survey area does not need to be as large as for CMR, and, because of this, many more surveys reach the guidelines for an optimally designed study. Only 15% of SECR studies had survey areas small enough to suggest moderate evidence of bias, and there was no evidence of bias due to inter-trap distance in SECR papers. This is partly because the guidelines for SECR are easier to achieve.

Efford et al. (2009) report that at least 20 captures are needed for a robust estimate from SECR (Zimmermann et al., 2012), which can be made up of any number of combinations of individuals and capture probability. But, despite only 15% of studies failing to reach a survey design guideline, almost 30% failed to achieve the 20 capture limit. This may imply that either the survey design guidelines produced by Tobler and Powell (2013) and Sollmann et al. (2012b) cannot be extrapolated to other species, or that other characteristics, such as densities, have a strong effect on the survey design and need to be taken into account. There was one estimate

calculated by SECR which was extremely large, over 10 000 animals/100km^2. This erroneously large overestimate would be relatively easy to spot, but using the classification system described above it was only rated as having moderate bias. As biased estimates will not always be as easy to identify as this particular example, it is important that care is taken to minimise the chances of inaccurate results by collecting sufficient data. More research is also required into when bias is introduced, to ensure that strongly biased estimates are accurately reported as such. Despite this, the SECR methodology shows less evidence of bias compared to CMR, and, therefore, there is a strong rationale for making it the default methodology. One caveat to this is that SECR is much newer and there have been fewer opportunities for researchers to explore its limitations.

2.4.3.3 Sample heterogeneity

If researchers do not record the details of the sample, it is difficult to tell whether there is large variation in capture probability, and, if so, from where the heterogeneity comes. Large variation in capture probability can be caused by one animal having more cameras in their home range than others, which can be modelled within SECR, or variation may be caused by camera placement that favours certain individuals over others, for example placing them on trails that are favoured by large males. This would required either a CMR M_h model or an adjustment in the SECR, for example to include a sex coefficient. However, despite calls for better recording of heterogeneity, studies rarely report these values.

One possible source of heterogeneity in the sample maybe that males are captured more frequently than females. This may be because they are more likely to walk on trails, where cameras are placed. Whilst a quarter of studies give the ratio of males to females, few give information on the number of male capture events to female capture events. In the data collected, there were more female individuals than male, which might be expected as for many species male territories overlap with several females (Sunquist and Sunquist, 2002). The information in the sample referring to the capture events for males and females is too limited to draw strong inferences but, despite there being more females surveyed, there are more

male capture events. The ratio of male to female captures, given the ratio of male to female individuals, is evidence that the current survey designs are significantly biased towards males because of their higher capture probability. This is taken into account with a CMR M_h model, or by splitting analyses into males and females, or introducing a sex coefficient into the model, all of which have been done previously. Sollmann et al. (2012b) and Gray and Prum (2012) have used SECR models in which males and females are modelled with different capture probabilities and activity patterns. However, if analyses require data to be split into multiple datasets in order to report robust results, this requires more data to be collected, and so much larger surveying efforts than are currently being performed.

2.5 Conclusion

Study design is poorly recorded in the literature, but the information that is available implies that the majority of current surveys are producing unreliable abundance and density estimates. In general, studies need to be larger and have higher trap densities. Current study designs have resulted in: small capture probabilities, low numbers of capture events and few unique individuals recorded. Common density estimation techniques, like CMR and SECR, produce unreliable estimates when this is the case. Furthermore, there is the potential that the study designs are collecting biased samples with higher capture probabilities for males than females. This means that only CMR M_h, or separate analyses for males and females would be appropriate.

From these results, the CMR methodology should not be used as a method of density estimation, as it is unlikely that researchers will have the resources to fulfil the surveying requirements. In addition, there is no reliable method for changing the abundance estimate into one of density. Therefore, it is desirable for SECR to be better understood, such that the following questions are answered:

- What effect does realistic movement patterns have on the the ideal survey design when using SECR density estimation? i.e. are the Tobler and Powell (2013) guidelines correct when movement assumptions are broken?

- Are 20 captures (made up of any number of individuals and recaptures) sufficient to estimate SECR density, or should there be more specificity in the number of individuals, and the number of recaptures?
- Is the distribution of captures and recaptures, across space and individuals, important for creating a good estimate of density?

Chapter 3

A flurry of activity: Modelling snow leopard movement

Contents

3.1 Introduction

The long-term monitoring of rare and elusive species such as the snow leopard (*Panthera uncia*) can be immensely challenging, and yet it is critical that we have robust estimates of their abundance to provide a basis from which to evaluate conservation measures (Legg and Nagy, 2006). Snow leopards are a good target species for the overall purpose of this thesis: they are difficult to monitor and, therefore, the ability to optimize survey designs for snow leopards is important for their conservation.

Spatially explicit capture recapture (SECR) models were developed, recognizing the need to allow for uneven spatial distributions of animals. However, SECR also relies on assumptions about animal movement (Borchers and Efford, 2008; Otis et al., 1978). If the assumptions about movement, including home range, do not match the reality, inaccurate, or imprecise, results may occur.

One of the central aims of this thesis is to assess the effectiveness and accuracy of monitoring methods given the challenges of working with extremely rare and wide-ranging species. This chapter uses tracking data on 18 snow leopards; this was obtained from Tom McCarthy and his team from Panthera (McCarthy and Johansson, 2013). The dataset is very large, and is one of the most compressive snow leopard datasets in the world; in this chapter it was used to create a realistic movement model.

The snow leopards were tagged with Global Positioning System (GPS) devices on special collars, and this data was used to make, and test, the movement

model described in this chapter. This provides a unique opportunity to examine a rarely-encountered species. This movement model will be used in later chapters to examine the reliability of SECR modelling on low density, far-ranging animals.

3.1.1 Review of GPS accuracy and data collection

GPS is used to monitor animals as it is highly effective at recording locations; it is spatially and temporally accurate (Tomkiewicz et al., 2010), and requires fewer human resources to be deployed than following species to determine their movement (Hebblewhite and Haydon, 2010). It also eliminates human biases, for example as the result of an inability to follow animals for long migrations, and allows for animals to be recorded in remote or inhospitable environments (Bjørneraas et al., 2010), as well as at night. For example, snow leopard behaviour was previously studied through radio telemetry, however they can produce significantly different results incomparison to GPS. Radio telemetry is limited by the ability of humans to get within close proximity, where as GPS uses satellites and is therefore a good method for monitoring animals. In particular, GPS is better for tracking snow leopards than radio telemetry due to their large home ranges and the difficult terrain they inhabit; however, there are a number of sources of error that can still occur which derive from their underlying methodology. In order to understand and use the data provided by Tom McCarthy and his team (McCarthy and Johansson, 2013) it is important to understand the mechanics and the accuracy of GPS.

There is a collection of 30 GPS satellites constantly broadcasting signals that are picked up by the GPS receivers used to monitor animal location. Based on these signals, a receiver can calculate how long it takes to get a signal from a satellite and, when they receive signals from at least four satellites the receiver can calculate it is approximate location using trigonometry. The more signals a receiver picks up, and the wider the satellite placement, the more accurate the estimate of the locations. This accuracy can be measured in part by dimensionality and the dilution of precision (DOP). Dimensionality is dependent on the number of satellites used to find the location: a location can either be a 3-dimensional (3D) fix, from 5 or more satellites, or a 2-dimensional (2D) fix, from at least 4 satellites. So many

satellites are needed because the theory assumes that time between signal send and signal received can be calculated accurately, however, in reality this would require an accurate clock on every GPS device. Instead, as this would be impractical and expensive, time can be added as an additional unknown to the GPS equations, and, with an extra unknown, the equation requires an additional data point to allow a solution to be found. 3D fixes are considered to be more reliable than 2D fixes (Rempel et al., 1995; Moen et al., 1996), and can therefore be kept in the sample. However, 2D fixes occur fairly frequently, with a range of errors caused by the spacing of the satellites used to triangulate the fix. For example, when satellites are far apart, the location is more precise unless the satellites are on the horizon, and vice versa. This spacing is measured by the DOP (Di Orio et al., 2003), and is calculated as the standard deviation of the location over the standard deviation of the inputs (Gopi, 2005). As datasets often have many 2D fixes, to maximise the power of an analysis the most reliable 2D fixes, as measured by the DOP, can be kept in the sample (D'Eon et al., 2002). DOP, however, does not explain all errors. Satellite signals can be disrupted by the ionosphere, or by signals reflecting off surfaces such as cliffs, in these cases DOP might suggest that the location is accurate when it is not (Stache et al., 2012). Animals also need to have a direct line of sight with the satellites in order to receive a signal; therefore, if they are in thick forest, in a crevasse, or even lying on the receiver, there can be missed captures.

Hebblewhite and Haydon (2010) wrote a critical review of GPS telemetry in ecology, in which they outlined the benefits GPS tracking would have on movement ecology, but also highlighted possible problems. They conclude that, overall, GPS would have a positive impact on ecology, with advantages in many fields, including: behavioural studies, migration patterns, home range estimation, and movement ecology. However one of their main concerns, which would affect almost every field of study, was the expense of such a system (Hebblewhite and Haydon, 2010). Whilst the cost per unit has reduced, there is a large cost associated with the manpower necessary for a successful deployment that may lead to small populations being sampled, which, in turn, can lead to biases in datasets (Cagnacci et al., 2010;

Hebblewhite and Haydon, 2010; Lindberg and Walker, 2007; Otis and White, 1999). Hebblewhite and Haydon (2010) also highlighted that GPS alone does not give any information about real behaviour, such as stalking other animals, that direct observation would (Davis et al., 1999), which may lead to a failure to make important inferences. One of the other disadvantages of GPS is that it is very power hungry, meaning that regular capture of animals, approximately every year for collar maintenance is required. The trade-off between high frequency captures and long term studies often results in the time between locations being lengthened so that recapture will not be necessary for many months (Mills et al., 2006); this larger temporal spacing means that detail of the movement is lost (Figure 3.1) (Musiani et al., 1998). Whilst some detail is lost at any frequency of fixes, this becomes more apparent with larger spacings. While a mixture of sampling regimes is possible, any period of high frequency captures will reduce the overall length of tracking. The spacing of GPS locations can interfere with inferences about animal movement; for example, a movement model could summarise an animal with fast tortuous movement as a slowly moving animal with strong direction (Laube and Purves, 2011).

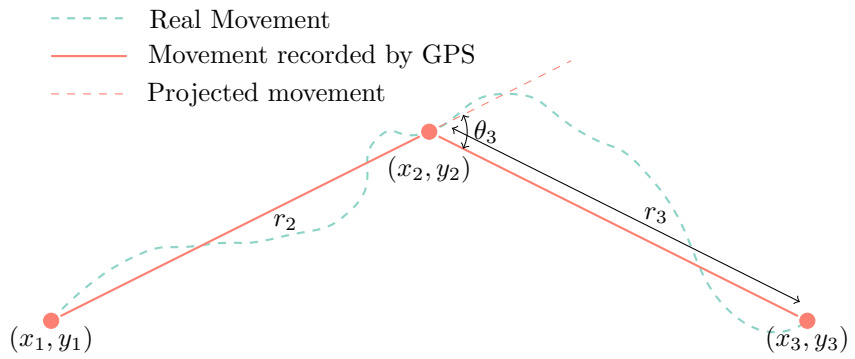


Figure 3.1: How GPS records real movement. Where dashed green line represents real movement, red points are GPS locations, and red lines are the movement paths estimated by the GPS data. The red dashed line represents projected movement if no change in direction is observed

It has been shown that a large sample of GPS data leads to a more accurate estimate of home range, resource use and movement models. For example Girard et al. (2002) showed that it was necessary to get at least 30-100 locations per season

in order to calculate the home range of moose using the minimum convex polygon (MCP). The minimum number of locations may vary by method of home range estimation as Seaman et al. (1999) found that only 30 to 50 locations per animal, over the period of the study would be needed using the kernel method. In addition to this, not only does there need to be a significant quantity of data from each animal (Otis and White, 1999), but Lindberg and Walker (2007) found that for even the simplest of studies, with binary outcomes, the sample size should be greater than 20 individuals, with over 75 for more complex studies. However, it is important to note that Lindberg and Walker (2007) do acknowledge that important results have been produced with smaller sample sizes. With low density species, such as snow leopards, it is difficult to capture 20 or more individuals.

While a large sample size is important for a good estimate of home range, and movement therein, it is also important to remember that if imprecise GPS fixes are not removed, incorrect inferences may be made (Bjørneraas et al., 2010). Frair et al. (2004), for example, found that GPS data which is biased due to terrain can lead to incorrect inferences about animal movement and resource use. In particular, that GPS error caused by the environment, in their case dense conifer forest, caused biases by reducing the number of successful GPS fixes. This, in turn, probably led to error in resource use models including type II errors in the distance to the trail (Frair et al., 2004). Even if an animal is stationary, the natural error in GPS fixes will always result in small positive distance travelled. This can lead to incorrect outcomes for animal movement models: Ganskopp and Johnson (2007) found that measures of distance travelled by cattle can be overestimated by 15%. Therefore it is important that erroneous locations be removed whilst maintaining the largest possible sample of animals and locations. D'Eon and Delparte (2005) state that the most common ways of screening locations are through the internal accuracy recordings of the GPS system, particularly the dimensionality of the fix and its dilution of precision. In a study on moose, Bjørneraas et al. (2010) found that excluding locations on just dimensionality and DOP was not enough to completely remove all the large errors from movement locations. As well as the dimensionality and DOP,

they also cleaned their data based on the speed between locations. If consecutive locations are very far apart, relative to the time between locations, the locations can be removed because, while individuals can move fast over short periods, over longer periods, these speeds are clearly unrealistic (Bjørneraas et al., 2010). In this study, a series of criteria for cleaning the data were developed based in the known problems of GPS. Locations that are inaccurate can be identified by using internal measures of accuracy, such as the dimensionality of the fix, or with calculated values, such as the speed between locations.

3.1.2 Movement parameters used in simulation methods

Models work by assigning statistical distributions to important parameters; for example, movement is often parameterised using two variables: step length, r, and turn angle, θ (Figure 3.1) (Jerde and Visscher, 2005). Step length is the distance between two known locations, whereas turn angle is the change in direction between two movement vectors, and therefore requires three known locations (Jerde and Visscher, 2005).

An important feature of movement for researchers studying density estimation is the size, and use, of home range. For example SECR has a parameter size of home range in the model itself (Borchers and Efford, 2008; Efford, 2004). In the original derivation of the SECR, there was an assumption that probability of capture was dependent on the distance to the centre of the home range (Efford, 2004; Borchers and Efford, 2008). Recent iterations of the methodology include heterogeneous landscapes where the environment within a home range is not uniform and the movement may not be centred (Royle et al., 2013b; Reich and Gardner, 2014), although whether this is needed is disputed (Efford, 2014; Royle et al., 2014).

All parameters in the model can vary between sex. For example, it is a common finding for felids that females typically have smaller territories than males (Sandell, 1989; Sollmann et al., 2011). They can also vary by season: for example snow leopards travel further in summer. Even after taking into account sex and season there may be large variation in movement parameters because of other environmental factors, including individual inclination. Therefore, it is often necessary to break down

the data into subpopulations, representing different sex and seasons, when devising movement models or when estimating density.

3.1.3 Movement modelling techniques

Given the exploratory nature of this study, and given that the precise mechanism that controls snow leopard movement is not known, multiple methods were examined to find the most appropriate technique. As, on average, camera trapping surveys last two to three months (Chapter 2), the simulation of movement only has to be able to replicate actual movement for this period of time.

Once the basic distributions of the distance, r, and turn angle, θ, have been calculated they can be used in a simple (correlated) random walk, a form of stochastic differential equation (SDE) (Preisler et al., 2004). SDEs are used to describe incremental movement. Most commonly in ecology, this only extends to the x and y planes, dX(t) and dY(t), although a third dimension, dZ(t), can be included if required (Brillinger, 2003). For a correlated random walk each new location is derived by displacement from the initial location by distance r and angle theta, where r and theta are drawn from random distributions. r and θ are often chosen from a normal distribution for distance and a wrapped distribution, although any suitable distribution could be used.

An analysis of step length and turn angle often shows patterns that can be classified into states of movement that correlate with behaviours (hunting, resting etc.) (Franke et al., 2004; Morales et al., 2004). Consequently, more complex models involving multiple correlated random walks may be developed to identify different behavioural states. State space models (SSM), and hidden Markov models (HMM), are complex models that categorise movement into such states, and assume that future movement is dependent on current movement characteristics (Patterson et al., 2008). Multi-state models were included in this chapter, as it is reasonable to assume that there may be behavioural states visible in the data. But whether, given the wide temporal spacing of locations, a time series analysis, or Markov process, would be most appropriate is not known. As a result, a cluster analysis was performed in order to find the number of states and the parameters of movement

associated with them, and multiple mechanisms for switching between states were examined. The number of states, and their parameters will be strongly affected by the resolution of the data.

Before any cleaning takes place on the data that will be used in a model, care must be taken to look at the assumptions of the model and what methods are appropriate. For example, in some SSM, there is an assumed error structure around each location (Anderson-Sprecher and Ledolter, 1991; Buckland et al., 2004; Jonsen et al., 2003, 2005), and, therefore, removing locations with large errors would affect the accuracy of the models as it would affect the estimation of internal parameters. In other modelling types, like HMM or SDE, it is assumed that each location is an accurate representation of the animal's location and that there is no such structure (Langrock et al., 2012).

3.1.4 The criteria for a good model, and model validation

In general, a model is a mathematical description of a naturally occurring process, often in a simplified form. The best models are good fits to real data, are as simple as possible, and can be used for prediction. In order to know whether these models replicate the important features of snow leopard movement, a process of validation must be untaken. One method is to split the data into two: a training dataset and a validation dataset. The training data is used to create the model, while the results are compared to the independent validation dataset. As the validation dataset has not been used to create the model, it should be suitable for comparison.

3.1.5 Hypotheses

In this chapter the following statements were tested:

- Sex and season will have a large impact on the movement of the snow leopards. This will be shown by greater differences between sexes and seasons than within sex and season
- Movement speed and directionality will form distinct clusters within the snow leopard movement data. These clusters of data may relate to discrete behaviours

- A correlated random walk will not be able to reflect the complexity of snow leopard movement. Movement states will be required to create a realistic simulation of snow leopard movement (defined below)

- Future movement will be influenced by the current movement state, and therefore memory past movements are necessary to simulate realistic movement (defined below)

3.2 Methods

3.2.1 Data cleaning

The original dataset was formed between 2008 and 2013, collected from the Tost mountains in Mongolia. Snow leopards were caught via foot-snares and then collared with GPS receivers from Vectronic. The data from the GPS collars was uploaded via satellite communication, as reported by Johansson et al. (2015). The dataset included 18 individuals and over 27,000 locations.

The collars were programmed to record their location once every 5 hours; however, under some circumstances, for example a poor signal, a new location would be collected at another time either soon after, or at a 1 hour interval. Therefore, there is not a continuous chain of locations all separated by 5 hours. The tags collected 29 different variables including latitude, longitude, and time of day, as well as the accuracy of each location, measure by DOP. All three movement models used in this thesis require the data to be cleaned in the same manner. The criteria used to remove imprecise, or outlying locations, are laid out in table 3.1.

Criteria	Details of when a location will be removed
Format	Incorrect formatting, e.g. Date_Time is not given in YYYY:MM:DD HH:MM:SS
Precision	A 2D fix and a $DOP > 5$
Speed 1	Where the speed of travel from the last recorded location is faster than the sprinting speed of a similarly sized species ($60\,\mathrm{km\,h^{-1}}$)
Speed 2	Where the time between locations is greater than one hour, and the speed of travel from the last recorded location is faster than the patrolling speed of a similarly sized species ($3\,\mathrm{km\,h^{-1}}$)

Table 3.1: Criteria for cleaning GPS data

The first, and simplest, part of cleaning process is to check that all the data is in the same, correct, format. The second part of data cleaning process is checking the precision of the data using the dimensionality and DOP of each location. All 3D fixes were kept in the sample, along with the most reliable 2D fixes as measured by the DOP. A location was considered to be unreliable and removed from the dataset when the standard deviation of the location is more than five times the standard deviation of the inputs; and therefore if the is DOP is greater than five, the location was deleted (Dussault et al., 2001; Rempel and Rodgers, 1997; Lewis et al., 2007a).

The final two methods in the cleaning process are based on the speed the animal is moving. The speed of the animal is calculated from a straight line between two consecutive points (methods used for this can be found in Appendix B.1), and is therefore the minimum speed at which the animal was moving. The maximum possible speed of an animal will vary with the timeframe. For example, over shorter periods of time, faster movement is more realistic since an animal may be sprinting. With snow leopards being difficult to find and follow in the wild, calculations of average speed are missing from the literature. However, McCarthy et al. (2005) believe that snow leopards in this area travel faster than other similarly sized felids, and so using values from other species provides a conservative estimate for maximum speed. Two speed criteria were used: a sprinting speed and a patrolling speed. Sometimes, in error, the GPS recorded two locations not at five hour intervals but closer together, if the speed needed to travel between these two locations was faster than the sprinting speed of a leopard (*Panthera pardus*), approximately ($60\,\mathrm{km\,h^{-1}}$) (Janis and Wilhelm, 1993) the newest location would be removed. The second criterion was said to be met if an animal moved faster than the patrolling speed of a leopard ($3\,\mathrm{km\,h^{-1}}$) for longer than an hour.

3.2.2 Data selection

There may be seasonal changes in snow leopard movement. In order to test this, the data was split into multiple seasons before analysis. As most camera trap surveys take place over two to three months (Chapter 2), the data was split into three month sections: a summer season (May, June, July) and a winter season (November, De-

cember, January). Summer and Winter were chosen, as under initial examination, these were the two time periods that showed the most coherent picture. The data is divided into blocks, which belong to a specific animal, season and year, where each block is taken as an independent section of data. By assuming independence there will be some unmodelled relationships that exist between blocks, including: age of the animal, whether females have cubs, and which from individual the data is drawn. Given the amount of data available, and the chance of overfitting the model, these relationships were left unexplored.

The blocks were selected, such that:

- Each block is data from 1 individual
- All locations are within 3 months of the start of the block (which creates multiple blocks per animal if the animal is surveyed for multiple years)
- Displacement and turn angles were calculated for locations with an approximate 5 h separation ($\pm$ 5 min)

Of the blocks that were created, 25% were selected at random to be the independent validation dataset and removed from the main data.

3.2.3 Exploratory data analysis

Before modelling took place on the data, an initial data analysis was performed. The data was split into subpopulations in order to examine whether sex and season do impact the patterns of movement. For this, the data was split into four subpopulations: winter males, winter females, summer males, summer females.

First, the displacement and turn angle were examined, as these variables form the basis of the use of space by an animal. The displacement was positively skewed, so in order to normalise the distribution of displacement, a log transform was performed. There were very few exactly stationary locations, which is expected as there is a small error associated with each GPS fix. A small value of 0.001 m was added to displacements of zero to avoid an infinite value when logged. The density distributions of logged displacement and turn angle were plotted using the density

function in R (R Core Team, 2014), and tested for variability between, and within, subpopulations. The variability between subpopulations was compared using the Kolmogorov-Smirnov test (K-S test). The within-subpopulation variability was assessed by pairwise testing the individuals within the subpopulation, using the K-S test with Bonferroni correction to correct for multiple testing.

In a correlated random walk, displacement and turn angle are independent. To determine whether this is true for snow leopard movement, a heat map of turn angle versus displacement was created to visualise any patterns.

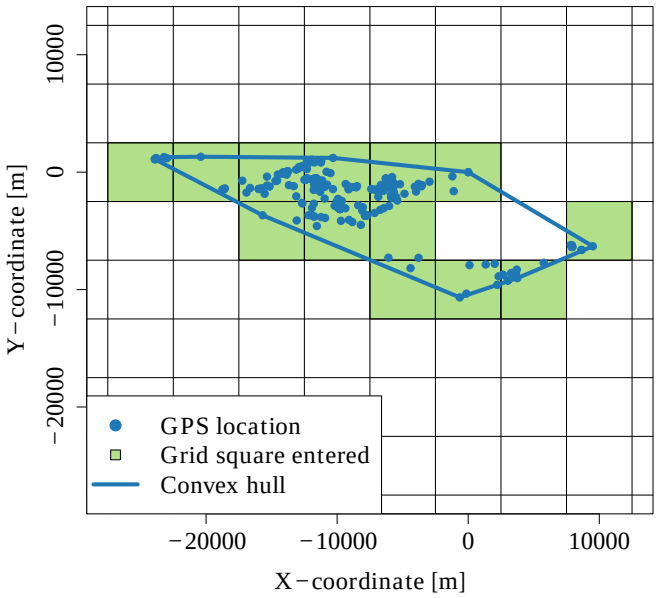


Figure 3.2: Example locations from one animal in the dataset showing the convex hull of the animal home range, and the occupancy level measured by the number of grid squares entered. Blue points mark GPS locations from an animal, and the blue line represents the convex hull. The white cells represent no registered occupancy, green cells represent at least one GPS location registered.

The next characteristic of interest is the size of home range. This was calculated using a 100% convex hull, the minimum convex polygon (MCP), which represents the smallest possible area that covers all the locations (Figure 3.2). The MCP is preferred over kernel density estimation (KDE) for this part of the analysis because it is the simplest method possible and relies on no arbitrary parameters. The density distribution of the logged area was plotted separately for each subpop-

ulation using the density function in R (R Core Team, 2014), and the K-S test was used to test for significant differences between subpopulations. The logged distributions of home ranges was used to reduce variance, and remove the long tail of the distribution. A log transformation is commonly performed on home range analyses, for example comparison between home range and body size (Kelt and Van Vuren, 2001), or home range and dispersal distance (Bowman et al., 2002).

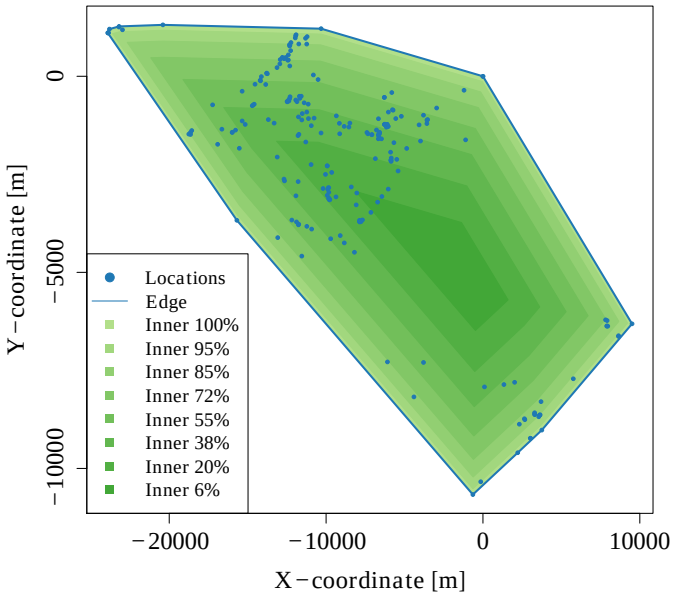


Figure 3.3: The convex hull of GPS locations with the percentage area from the centre marked. Blue points mark GPS locations from an animal, the blue line represents the convex hull and darker shades of green represent areas closer to the centre.

Next, the snow leopard use of home range was assessed to see whether it follows the assumption of the SECR methodology. Namely that the majority of the movement is at the centre of the home range, and that this movement reduces with distance to the centre in a predictable mathematical way. To test this, the home range was split into bands, similar to those shown in figure 3.3, where the bands form concentric polygons around the centre of the home range. The number, and percentage, of locations within each band were calculated. By calculating bands with equal area, the percentage of the locations within each band are comparable; as a result, the proportion of time spent in the outer area of home range compared

to the inner area can be calculated. In this analysis, the area of each band was set to four percent of the total area. As each band has the same area, if there were an equal number of locations in each band, the individual would be spending approximately the same amount of time in all parts of its home range. If the percentage of locations were to be plotted against the band in which they were recorded, this would form a line. If the movement follows the model set out in SECR then the percentage of locations would be higher in the inner bands, and would therefore form a curve.

Lastly, a measure was created to capture the amount of the home range the snow leopards occupies, later called the occupation level. One possible method of measuring the space a snow leopard occupies would have been to use the KDE, as it can calculate the home range used by an animal with lower bias than other methods such as MCP and bivariate-normal methods (Gitzen et al., 2006). However, some of the current literature, such as Kie et al. (2010), questions whether this is now an appropriate methodology given that with GPS we know the exact placement of animals. In addition, KDE can produce misleading results if the arbitrary choice of bandwidth, and bandwidth methodology, performs poorly (Gitzen et al., 2006). Another problem with both standard KDE and MCP is that it smoothes the home range into areas that animals may not occupy, such as the land across rivers. Benhamou and Cornélis (2010) solved this problem by creating a method that included natural barriers within the framework of the KDE; however, without having *a priori* knowledge of what and where the barriers to a snow leopard are, it is not possible to replicate this analysis. Therefore, in this chapter, the method of assigning territory blocks outlined below. The landscape is broken down into squares, and the number of squares an animal entered was counted. An arbitrary decision was made to make these squares 5 km $\times$ 5 km; however, the choice of square size made little difference to the inferences made about use of space (compared to 1 km $\times$ 1 km and 10 km $\times$ 10 km). This measures how many different areas the animal visits (Figure 3.2), and is of interest as it is a measure of how much of the territory is used by the snow leopard. The distribution of the occupation level was plotted separately for each

subpopulations using the density function in R (R Core Team, 2014), and they were compared using the K-S test.

3.2.4 Movement models

Three different models were used on the training data for the male and female summer subpopulations. The first movement model was a correlated random walk, where the mean and standard deviation of the logged displacement and the turn angle were calculated from the dataset.

The second and third model were based on behavioural states in the data. To find the optimal number of behavioural states, the Rmixmod (Auder et al., 2014) clustering algorithm was used. In order to test the robustness of the clusters, alternative clustering methods were used and the new clusters were compared with the Rmixmod clusters in order to see whether similar results were produced. The Rmixmod package was chosen as the methodology used in the body of this chapter as it provided additional functionality over other clustering methods, such as seeding initial random values. In order to calculate the clusters the Rmixmod model maximises the likelihood of the probability density function (3.1).

$$f(x_i, \theta) = \sum_{k=1}^{K} p_k h(x_i|\lambda_k) \tag{3.1}$$

Where k is the number of clusters, and, in this analysis, h is a Gaussian distribution with mean μ_k and variance Σ_k, so that $\lambda_k = (\mu_k, \Sigma_k)$.

The Rmixmod package produced the following parameters:

- The number of clusters in the data, n
- The probability of being in each cluster, $\mathbf{p} = (p_1, \ldots, p_n)$
- The location of the centre for each for each cluster

$$\mu_i = \begin{bmatrix} \mu_{R_i} \\ \mu_{\Theta_i} \end{bmatrix} \text{ for i=1,...,n}$$

Where μ_{R_i} is the mean distance, and μ_{Θ_i} is the mean angular change for state i

- The variance-covariance matrix for each for each cluster

$$\Sigma_i = \begin{bmatrix} \sigma_{R_i,R_i,} & \sigma_{R_i,\Theta_i,} \\ \sigma_{\Theta_i,R_i} & \sigma_{\Theta_i,\Theta_i,} \end{bmatrix} \text{ for i=1,...,n}$$

  Where $\sigma_{R_i,R_i,}$ is the variance of distance, $\sigma_{\Theta_i,\Theta_i,}$ is the variance of angle, and $\sigma_{R_i,\Theta_i,}$ is the covariance of distance and angle for state i.

In all the movement models, the maximum allowed distance between two locations was 15 km, based on the maximum patrolling speed for a similar sized felid (Table 3.1). In the data cleaning that occurred earlier this was specified as the maximum displacement which could reasonably be expected of a snow leopard over 5 hours. It is necessary to include a maximum distance between locations in the model as simulations will be done over many thousands of replicates and eventually an extreme number will occur.

The mechanism for switching between states was modelled using two different methods, non-Markovian transitions and Markovian transitions. Creating the Markovian transition model from the clustered data rather than using a HMM allows a comparison between the types of transitions, rather than between two separate sets of clusters. The second model used non-Markovian transitions between states. At each step, a new state was chosen based on the overall probability of being in each state, $\mathbf{p}$.

The third movement model used Markovian transitions. The Markov principle is that the probability of going from state i to state j at time $t+1$ is only dependent on the current state, not on previous states. The Markov matrix in this model was calculated from the classification of training states provided by Rmixmod (using the maximum likelihood method).

The movement in the second and third movement models was bounded by a circle five times the area of the largest home range in the training dataset. This bound was intended to stop an animal moving too far away from its start location, without artificially constraining the animal to a circular home range.

None of the models include a time of day effect, even though a previous snow leopard study by McCarthy et al. (2005) noted that snow leopards are more likely

to be active at certain times. The McCarthy et al. (2005) study was was based on radio telemetry and active following of snow leopards, which allowed for consistent capturing regardless of the time of day. However, the data for this study comes from GPS locations where the spread of missing locations is not even, possibly as a result of behaviour changes; for example an animal sleeping is likely to result in a missed location (Graves and Waller, 2006; D'Eon and Delparte, 2005). Therefore inferences that can be made about the effect of time of day on behaviour are masked by the number of missed locations that occur.

3.2.5 Validation of the model

After each model was generated, they were used to create simulated movement data to which validation metrics were applied (Table 3.2). These were compared to the metrics performed on the independent validation datasets. As the validation data is not used to create the model, any patterns seen in the model output can be compared to the validation data to check whether the simulation model can create movement features that appear in real life. If the results from validation metrics on the validation dataset and the simulation data were statistically similar, then this would imply credibility for the model produced. The validation data was chosen at random to avoid the possibility of choosing validation data to fit the model results. This method of validation was chosen for its simplicity and effectiveness.

The metrics were designed to characterise the important features of movement, including the features that are important in estimating animal density. The metrics were based on five criteria: displacement and turn angle over 5, 10, and 25hrs, size of home range, use of home range and occupation level. In order to know whether the model replicates important features of the space use and movement this was simulated for 1000 animals for three months. The simulated movement was compared to the distributions of movement in the validation dataset based on a series of metrics (Table 3.2).

Metric name	Description of the metric	Test performed on metric
Displacement	Distribution of displacement between locations that are separated by 5hours (1 step), 10hours (2 steps) and 25hours (5 steps)	K-S test
Turn angle	Distribution of turn angle between locations that are separated by 5hours (1 step),10hours (2 steps) and 25hours (5 steps)	K-S test
Size of home range	Size of home range, measured by the 100% convex hull	Visual
Use of home range	The amount of space occupied by the animal, by measuring the number of 5km squares the animal enters (Figure 3.2)	Visual
Occupation level	How the territory is used, measure by the amount of time spent in each band of the home range (Figure 3.3)	Visual

Table 3.2: Description of the validation metrics used to assess movement models

3.3 Results

3.3.1 Data cleaning and selection

Using the criteria laid out in table 3.1, the size of the dataset was reduced by 21%, to just over 22000 fixes from 14 animals. Most of the excluded locations occurred because dimensionality and DOP were incorrectly stored so that it was impossible to evaluate their accuracy (Table 3.3). After the removal of incorrectly formatted points and 2D fixes with high DOP, there were no movements with improbably high speeds left in the dataset.

Cleaning criteria	Number of locations	Number of animals	Date range	Number of deleted locations
-	27,906	18	Aug 2001 - Aug 2013	-
Format	22,861	18	Feb 2010 - Aug 2013	5,045
Precision	22,015	14	Feb 2010 - Aug 2013	846
Speed1	22,015	14	Feb 2010 - Aug 2013	0
Speed2	22,015	14	Feb 2010 - Aug 2013	0

Table 3.3: Number of animals and locations after data cleaning

For the summer subpopulations there were 12 animals, 5 males and 7 females, forming 20 individual blocks of data (Table B.2). Blocks S05, S10 and S12 were selected as validation for females and S13 and S17 were selected for validation for the males (for block definitions see Appendix B, Table B.2).

3.3.2 Initial exploratory analysis of the data

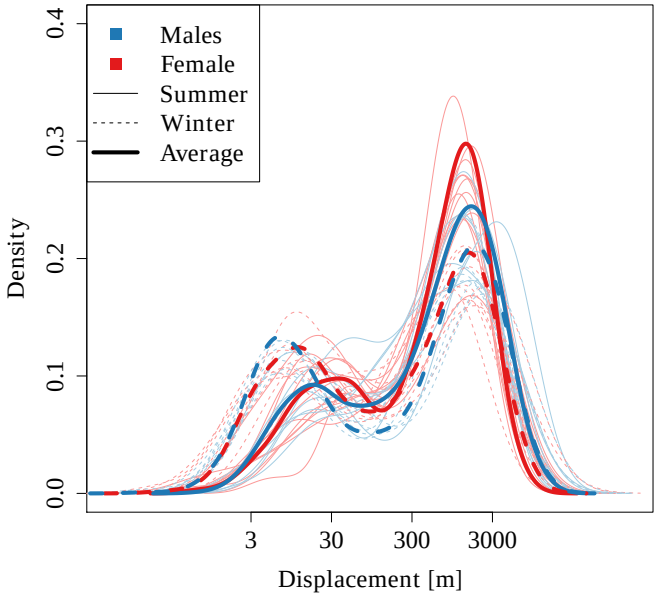


Figure 3.4: The density of the logged displacement for locations 5 hours apart. Fine lines represent individuals, and thick lines represent subset averages. Females are red and males are blue, and dashed lines are winter and solid lines are summer.

There are two distinct peaks in density for logged displacement (Figure 3.4). For all subpopulations there was a low peak for small displacement, and a higher peak for large displacement. However, the average distribution of each subpopulation was significantly different from all others (summer male vs winter male, p-value < 0.001; summer female vs winter female, p-value < 0.001; summer female vs summer male, p-value < 0.001; winter female vs winter male, p-value = 0.002). Small movements are more common in winter than summer. In addition, small displacements in summer are larger than small displacements in winter. For example, the value for small displacements is approximately 10 m, whilst in summer it is 30 m - 40 m. Even within subpopulations (summer males, winter females, etc.) there are significant differences between displacement distributions for individuals: even after correcting for multiple testing, 6% of the combinations were significantly different (Tables B.5 - B.9).

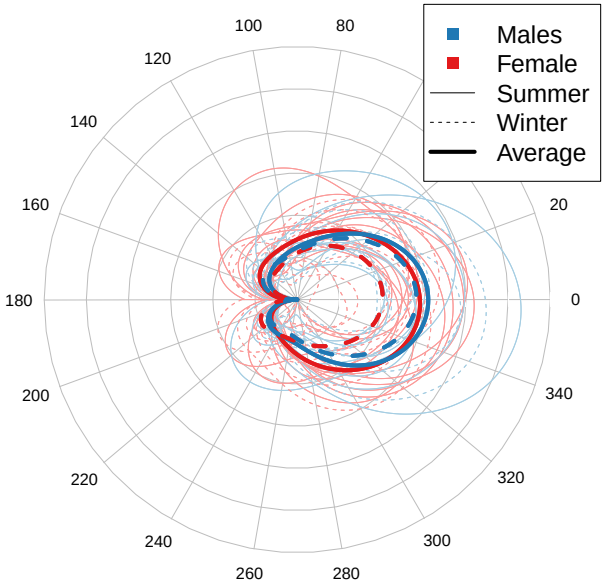


Figure 3.5: The density of the turn angle for locations 5 hours apart. Fine lines represent individuals, and thick lines represent subset averages. Females are red and males are blue, and dashed lines are winter and solid lines are summer.

The density of the turn angle between movement vectors has two peaks. These correspond to no change in direction, and reverse direction, centred on 0° and 180° (Figure 3.5). When looking at turn angle there was no significant difference between subpopulations (summer female vs summer male, p-value = 0.22, winter female vs winter male, p-value = 0.31; summer male vs winter male, p-value = 0.45; summer female vs winter female, p-value = 0.53). There is also little difference within subpopulations; after correcting for multiple tests there are no significant differences between individuals within the four subpopulations.

Displacement and turn angle are dependent on each other, with higher turn angles associated with lower displacements and vice versa (Figure B.1a, Fig. B.1b, Fig. B.2a, Figure B.2b). This is more evident in the winter subpopulations, and may be due to the larger proportion of smaller movements being recorded in that season.

The distribution of home range areas, as measured by the 100% convex hull have a positive skew (Figure 3.6). The range between 49 km^2 and 879 km^2, and did not differ significantly between subpopulations (summer males vs summer female,

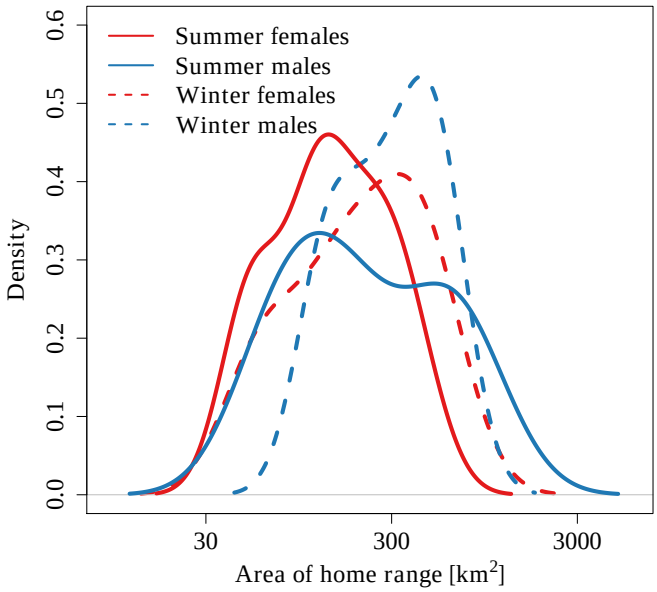


Figure 3.6: The density distribution of the logged area of the convex hull. Females are red and males are blue, and dashed lines are winter and solid lines are summer.

p-value = 0.45; winter males vs winter female, p-value = 0.65; summer males vs winter male, p-value = 0.51; summer females vs winter female, p-value =0.43).

There is a large variation in the amount of time individuals spent in each band of their home range within subpopulations. For example, some individuals spent substantially more time in the inner bands of the home range, whilst others appeared to live on the edge. On average, all subpopulations had a similar pattern of home range use, with an approximately equal amount of time spent in each band of the home range. This pattern implies that there is much greater variation within subpopulations than between subpopulations (Figure 3.7), and this is interesting as it shows that on this scale there is no systematic difference in the way females and males use the space which can be seen in other species.

The final measure of home range use is occupation level (as calculated in section 3.2.3). The distribution for occupation level has a slight positive skew. This pattern was seen consistently between subpopulations (summer males vs summer female, p-value = 0.78; winter males vs winter female, p-value = 0.94; summer males vs winter male, p-value = 0.78; summer females vs winter female, p-value

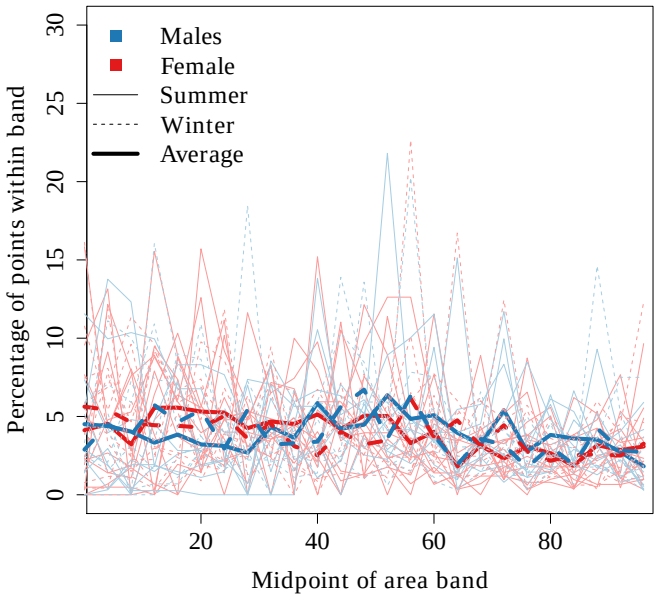


Figure 3.7: Number of locations plotted against the distance from the centre of the home range. Fine lines represent individuals, and thick lines represent subset averages. Females are red and males are blue, and dashed lines are winter and solid lines are summer.

=0.51). If an alternative grid size were to be, for example 1km grid spacing, then there would still be no significant differences between the subpopulations (Table B.4).

3.3.3 Results of the modelling

3.3.3.1 Results of the summer season

For the random walk model, the mean and standard deviation for the logged displacement and turn angle were calculated for males and females. The average speed, and turn angle, of the sexes were not significantly different for the summer months (Table B.2). The turn angle was centred around 0° and the average displacement per 5 hour period was approximately 1200 m, although both of these was associated with large levels of variance (Table B.10).

Using the Rmixmod clustering algorithm, four clusters for males (Figure 3.9), and five clusters for females (Figure 3.10), were found in the summer data. The parameters of these clusters can be found in Appendix B.5. Both sexes have similar

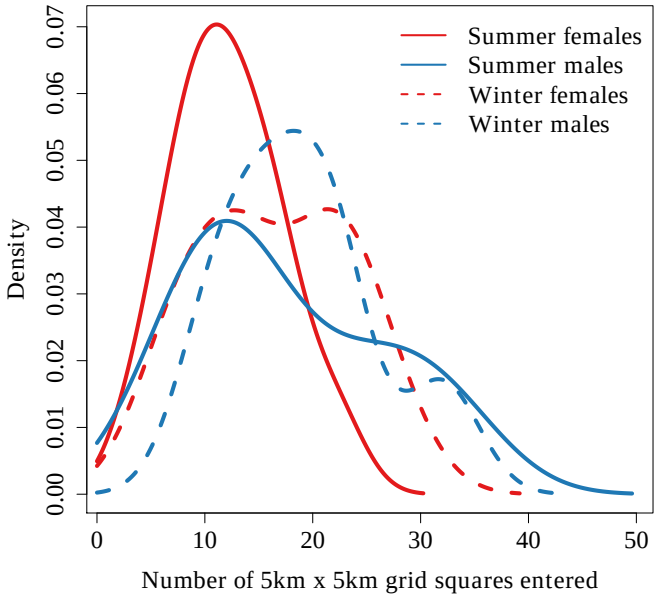


Figure 3.8: The occupation levels of home ranges. Females are red and males are blue, and dashed lines are winter and solid lines are summer.

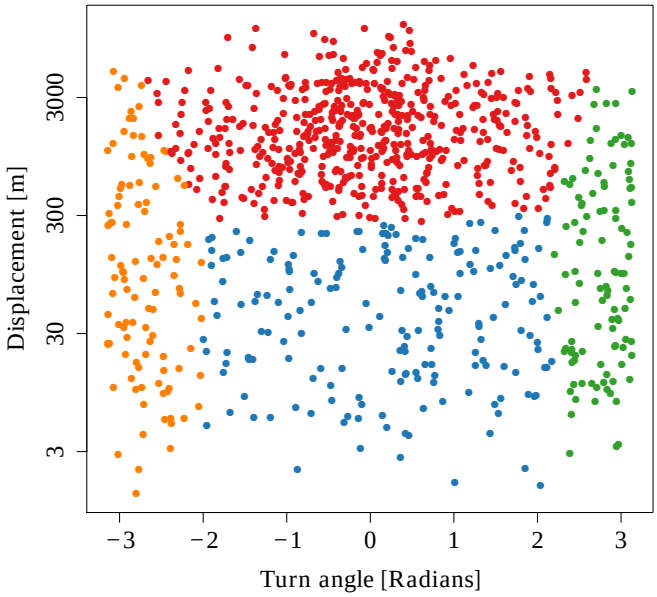


Figure 3.9: The clusters of movement found in the male movement, where colours represent different clusters derived from Snow Leopard GPS locations

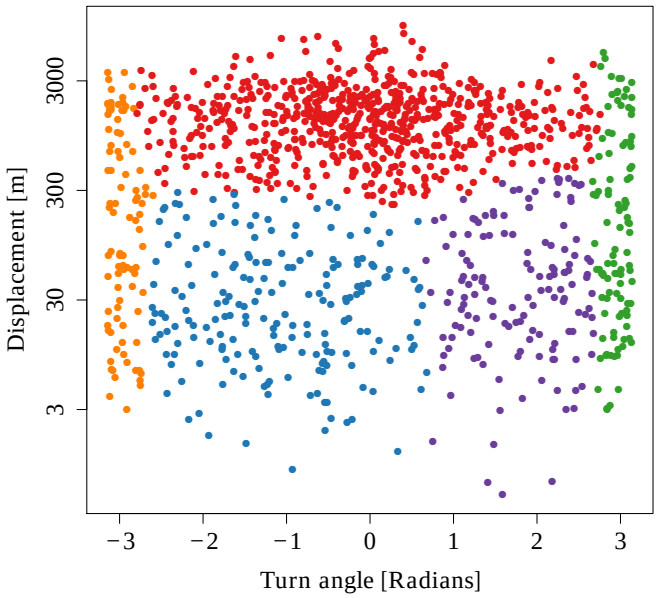


Figure 3.10: The clusters of movement found in the female movement, where colours represent different clusters derived from Snow Leopard GPS locations

clusters with the only difference being that the slow movement with little change in direction cluster in the males is split into two clusters for the females. The split in the cluster appears to be almost in the centre and therefore represents slow movement in clockwise and anti-clockwise directions.

The red clusters in figures 3.9 and 3.10 represent forward movement where an animal travels more than 300 m from its start location within a 5 hour period. Stationary or slow, movement where the animals move less than 300 m (for females this is shown as two clusters), is represented by blue clusters and blue and purple cluster for females. Finally, both males and females have backtracking movement, where an animal moves the opposite direction to the previous location, represented by orange and green clusters. The orange and green clusters represent the same type of movement, just in different directions. Whilst these clusters are not obviously distinct, other clustering methods gave similar results to those found by this method so the clusters that were found are not just artefacts of one particular methodology (Figure B.3a, and Figure B.3b).

3.3.4 Validation results of the summer season

In order to examine the ability of each model to replicate important features of movement, the models were used to simulate data. Examples of the simulated movement paths for each model and validation dataset can be found in Appendix B.6 (Figure B.4a - B.5d).

3.3.4.1 Displacement

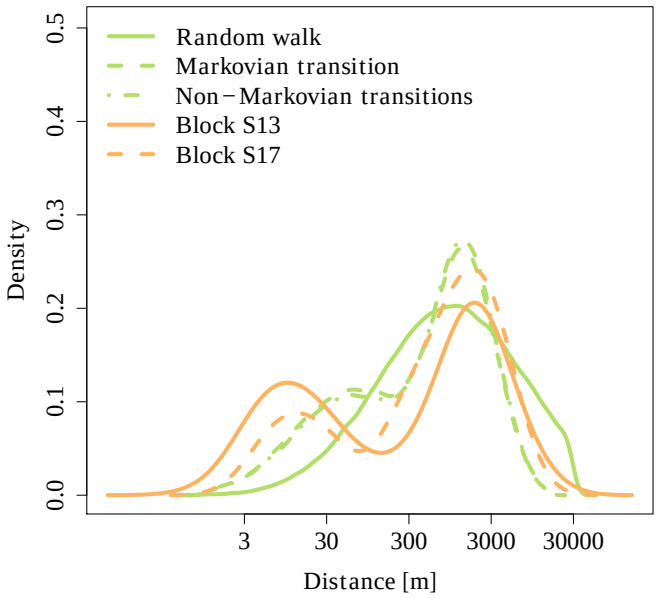


Figure 3.11: The distribution of displacement after 5 hours for males. Green lines and orange lines representing simulations and validation data respectively

The cluster-based models, for both sexes, were able to replicate the bimodal distribution found in the validation dataset (Figure 3.11 - Figure 3.12); however, the random walk produced an approximately normal distribution truncated at 15 km. There is a better fit to the validation dataset for female simulations than the male simulations, with the lower peaks occurring in approximately the same place for female movement but not for male movement. It should be remembered, however, that the displacement between individual blocks is significantly different (Figure 3.4), and, therefore, obtaining a model which matches all the data may not be possible within the models selected.

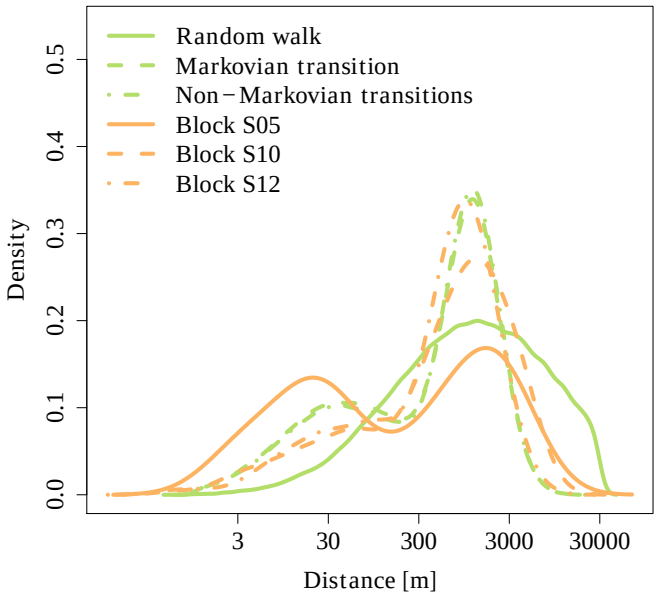
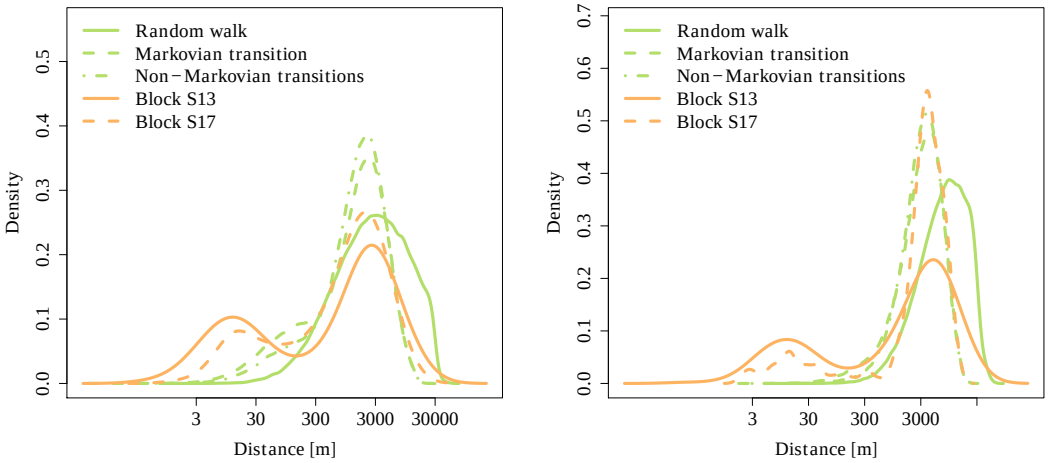


Figure 3.12: The distribution of displacement after 5 hours for females. Green lines and orange lines representing simulations and validation data respectively

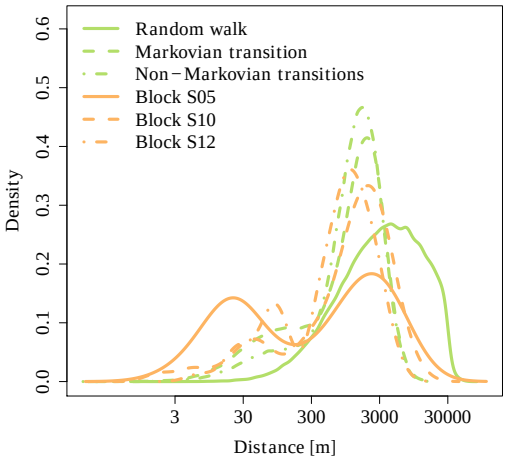
In the longer term, none of the simulations match the displacement in the validation dataset. The displacement when locations are separated by 25 hours still has a bimodal distribution in the validation data, implying that the movement does not follow a Markovian process as there is memory in the system (Figure 3.13b, Figure 3.13d). The expected amount of time in each state would be dependent on the probabilities in the Markov chain. If the Markov chain has absorbing states, for example where an animal in a stationary state remained in that state, then we would expect to see animals stay in the same state. Here, we would expect animals to switch between both stationary and moving states, and therefore, after multiple iterations, one would expect all or most of the animals to have moved away from their initial location.

This bimodal distribution found in 10 and 25 hour separated data is not replicated by any of the models (Figure 3.13b, Figure 3.13d). Even when locations are only separated by 10 hours, the size of the low displacement peak from Markovian transitions is not as large as the peaks in the validation dataset. The non-Markovian

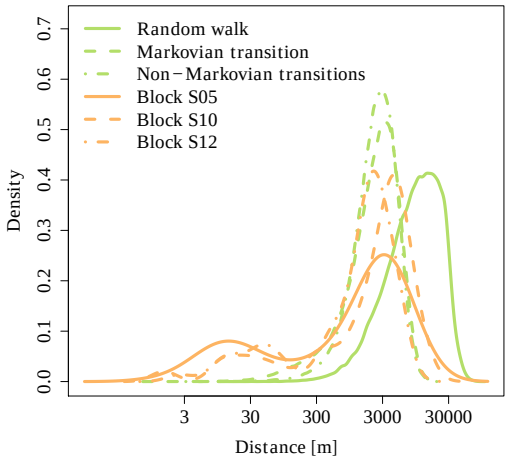


(a) Displacement after 10 hours, males

(b) Displacement after 25 hours, males



(c) Displacement after 10 hours, females



(d) Displacement after 25 hours, females

Figure 3.13: The distribution of displacement after a) 10 hours for males, b) 10 hours for females, c) 25 hours for males and d) 25 hours for females. Green lines and orange lines representing simulations and validation data respectively

transitions produces a heavy tail at 10 hours of displacement rather than a bimodal distribution (Figure 3.13a, Figure 3.13c).

3.3.4.2 Turn angle

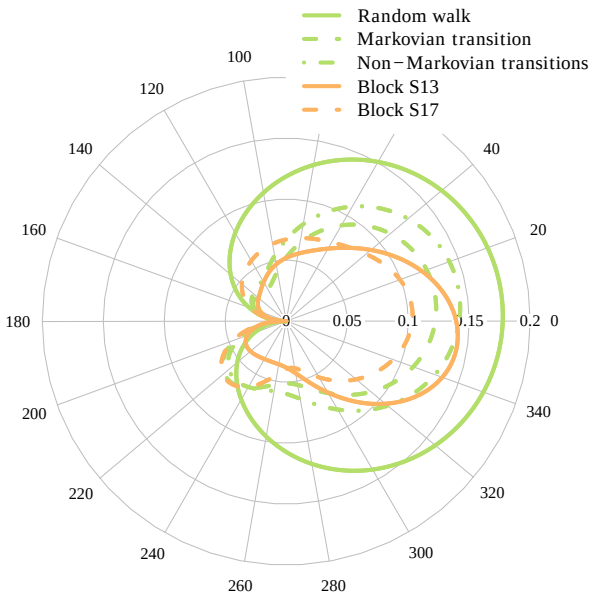


Figure 3.14: The distribution of turn angle after 5 hours for males. With green lines and orange lines representing simulations and validation data respectively

In all the validation datasets, the distribution of turn angle between movement vectors is not symmetrical. However, a pattern showing a cluster around 0° is visible. This movement is replicated in both the cluster-based simulations, and the random walk (Figure 3.14, Figure 3.15).

When locations are separated by 10 hours or by 25 hours, any patterns are difficult to see. There is a large amount of variation in the validation data as only a small number of locations are separated by 10 and 25 hours (Figure B.6a, Figure B.6c, Figure B.6b, Figure B.6d). From this measure there is no way of telling whether the simulations adequately capture the medium term turn angles.

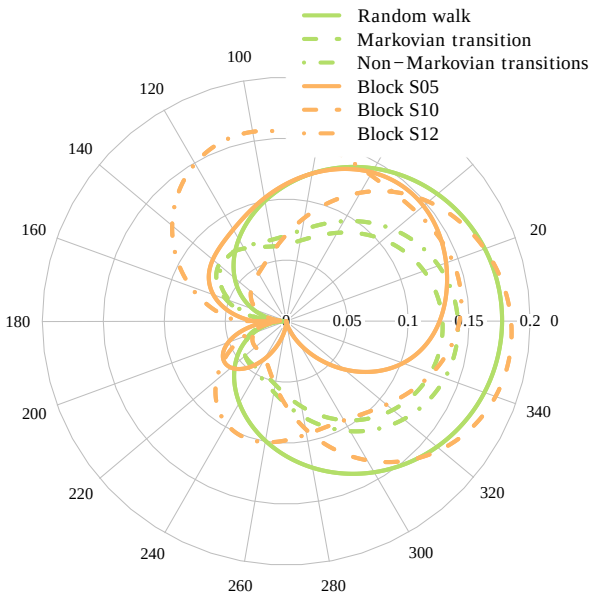


Figure 3.15: The distribution of turn angle after 5 hours for females. With green lines and orange lines representing simulations and validation data respectively

3.3.4.3 Size and use of home range

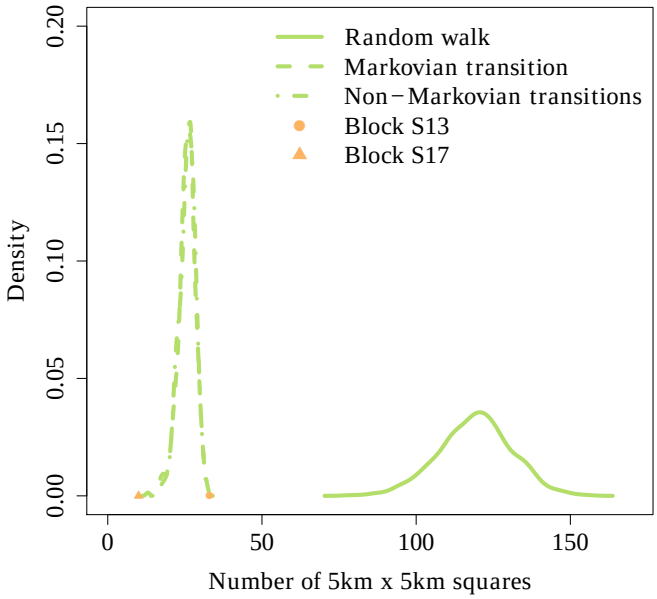


Figure 3.16: The distribution of number of number of grid squares entered for males. With green lines and orange points representing simulations and validation data respectively

The occupation levels for males and females has approximately symmetrical distribution for all simulation methods. The distributions of occupation measure for both clustering models have approximately the same mode and width, but the distribution for the random walk model has a much higher modal value and larger variance. (Figure 3.16, Figure 3.17). All of the validation points are close to, or within, the distribution of occupation levels from both cluster based models, with the male validation points on either side of the distribution, and the female validation points occurring in the bottom half of the distribution. This tends to suggest that the clustering models produce levels of occupation that are plausible, but the random walk produces unrealistically large levels of occupation.

For each model type, the logged area of the MCP home range in the simulated output follows an approximately normal distribution. The clustering models, with Markovian and non-Markovian transitions, produce distributions centred on approximately the same value; however, the areas produced under the random walks

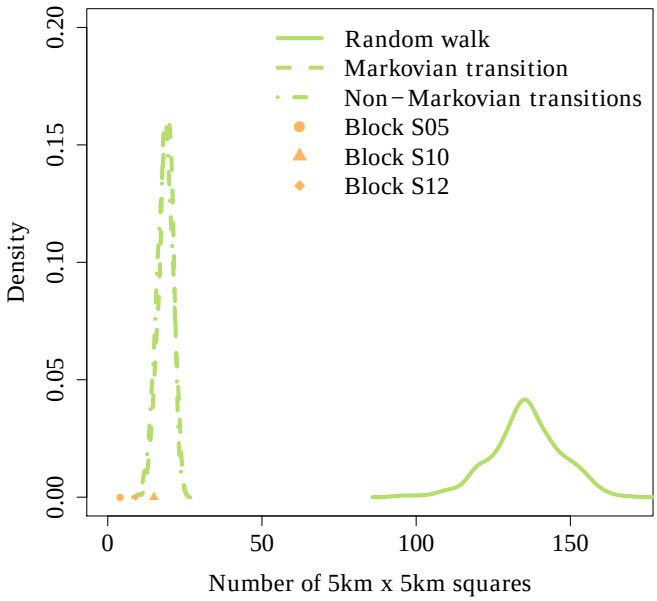


Figure 3.17: The distribution of number of number of grid squares entered for females. With green lines and orange points representing simulations and validation data respectively

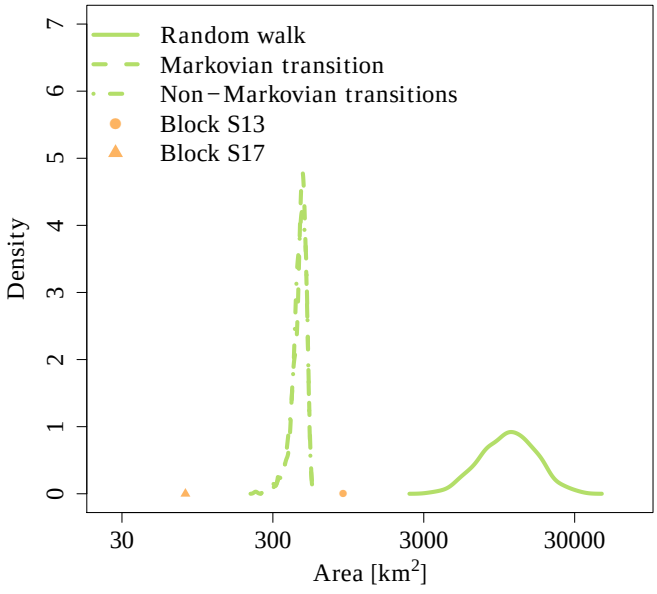


Figure 3.18: The distribution of the logged home range area for males. With green lines and orange points representing simulations and validation data respectively

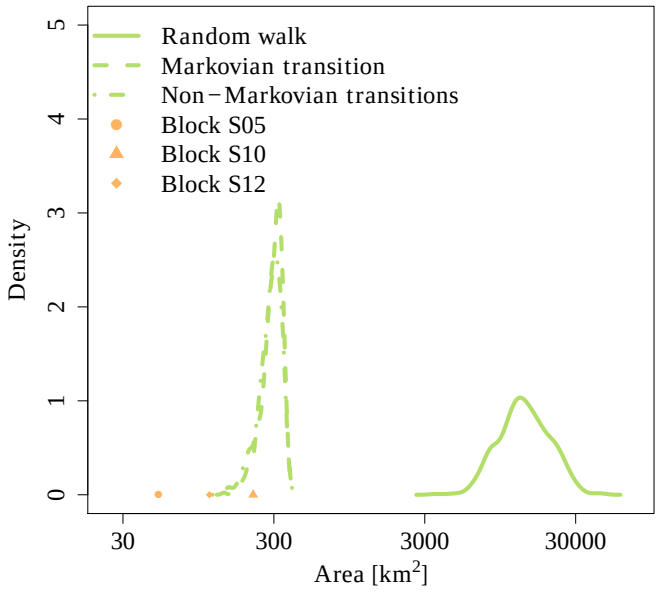


Figure 3.19: The distribution of the logged home range area for females. With green lines and orange points representing simulations and validation data respectively

is much larger. For both sexes, areas generated by the either cluster model are more consistent with the validation data, with the validation data falling either side of, and on the lower half of, the distribution created by clusters for males and females respectively (Figure 3.18, Figure 3.19). As with the occupation measure above, the random walk produces areas that are too large to be realistic.

The use of the home range was similar across all simulations, with an animal being equally likely to be in any band of its home range. The simulations produced a large range of results, but the random walk simulations produced a substantially wider range than the cluster models. In general, the validation data fell mainly inside the range of simulations produced from both the cluster models (Figure 3.20, Figure 3.21).

3.4 Discussion

Some important features of snow leopard movement were successfully modelled using clusters to represent different behaviours. For this thesis a good model of snow leopard movement must allow for simulations of the animals for 3 months, includ-

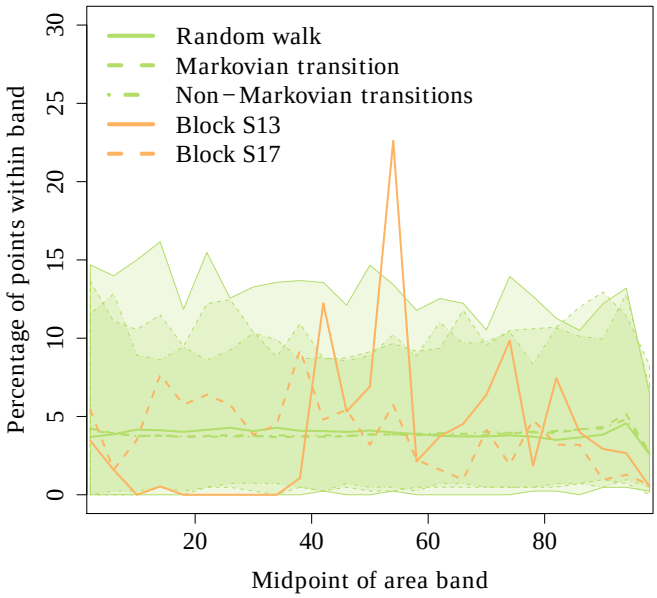


Figure 3.20: The home range use distribution for males, where the green shaded area represents the range of percentage points, and thick green lines representing the average across all simulations; with plain line, dashed line and dotted line represent random walk, clusters with Markovian transitions, and clusters with non-Markovian transitions respectively, and where the orange line represents blocks of validation data.

ing: their movement displacement and turn angle being within realistic bounds, and the distribution of the movement over the home range being realistic. By using a movement cluster approach, the size, and use, of home range was adequately replicated, along with short term movement patterns. This should allow successful exploration of the density estimation models in the next chapters of this thesis (Chapter 4).

3.4.1 Data cleaning and preparation

After cleaning, the data comprised over 22,000 locations from 14 animals; where the majority of removed locations were mis-formatted (Table 3.3), with some collars consistently storing data incorrectly. This resulted in the records of these animals being removed from the dataset, and this reduction in animal numbers may have resulted in decreased ability to see natural variation within the population. It is generally understood that maximising the number of animals in a study is necessary

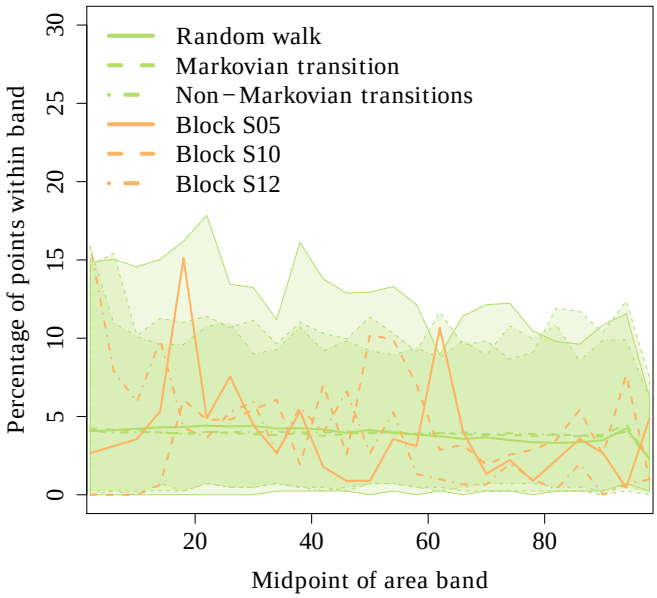


Figure 3.21: The home range use distribution for females, where the green shaded area represents the range of percentage points, and thick green lines representing the average across all simulations; with plain line, dashed line and dotted line represent random walk, clusters with Markovian transitions, and clusters with non-Markovian transitions respectively, and where the orange line represents blocks of validation data

for a robust result (Otis and White, 1999; Börger et al., 2006; Lindberg and Walker, 2007). But, given the extreme rarity of snow leopards (Jackson et al., 2008) it would be extremely difficult to capture and survey a larger number of animals than is included in this study. Having access to McCarthy's data (McCarthy and Johansson, 2013) represented an unprecedented opportunity for modeling snow leopard movement patterns.

No data points were deleted due to either speed criteria, as no animal have displacement large enough. However, using a proxy species for these values is not ideal. Whilst McCarthy et al. (2005) report that snow leopards move faster than similarly-sized species such as leopards, difficulties in the terrain may stop straight-line movement meaning that smaller displacements may be unrealistic. The terrain that these animals are living in is far from flat, and any distance travel will likely involve large changes in gradients, therefore even if an animal did travel in a direct

line between two point then the distance travel would still be larger than is measured here.

If too many parameters are used to create a model, then overfitting may result. To avoid this, a general rule of thumb is that the size of the input should be at least 10 to 30 times the number of parameters (Van Niel et al., 2005; Piper, 1987). The data used to create the movement model was made up of six blocks of male data (980 locations) and nine blocks of female data (1393 locations), meaning that any model should have a maximum of 98 parameters. The clustering model with Markovian transitions required the most parameters, 49 and 61 parameters for males and females respectively. Therefore, even for the most complex model, the dataset should be large enough to avoid overfitting, but more data and ideally closer to 33 parameters would make this clearer.

In order to estimate home range accuracy, it was necessary to collect at least 30 -100 locations per season per individual (Girard et al., 2002). Each animal had between 54 and 252 locations, with the majority of blocks containing more than 150 locations. Therefore, the home range analysis should have enough data to create a good estimate of home range area.

Given occasional missed fixes, the temporal spacing of the remaining fixes is variable. Fixes were analysed as if they were missing at random. However, the nature of the dataset implies that this may not be true. Fixes are more likely to be missing in certain geographical locations (e.g. under cover) (Schlägel and Lewis, 2014), or because of animal behaviour (e.g. sleep) (Graves and Waller, 2006; D'Eon and Delparte, 2005). This may have led to incorrect modelling of the movement, and therefore incorrect inferences about snow leopard behaviour. The analysis was performed on 22,000 locations, and this is a large sample. Moreover, GPS is one of the most effective method of remote monitoring available, and the results outlined in this chapter should be reliable.

The independent dataset used for validation was made up of two blocks of male and three blocks of female data. Using multiple blocks of data for validation gives a range of realistic possible movement patterns from different animals. However, as

there is a large amount of variability between subpopulations it may be impossible to replicate the movement patterns in all the validation blocks.

3.4.2 Snow leopard movement

The exploratory analysis produced evidence that supported the the idea that snow leopards perform different types of movement. In all subpopulations, at a five hour scale, there are at least two states of movement evident in the displacement and turn angle. Despite there being a significant difference between, as well as within, subpopulations, the two states in displacement were similar across individuals and represented a stationary behaviour and travelling behaviour. Differences in the distribution of displacement for season and sex is important to replicate in later movement models as speed is an important factor in capture probability (Lucas et al., 2015). The distribution of turn angle was similar across all subpopulations, with two peaks, representing forward and backwards travel. Heat maps of displacement and turn angle showed that they were not independent and so, as there is a relationship between the two variables, they should be modelled together. However the true relationship between turn angle and displacement is obscured by the sampling frequency. At a higher sampling frequency it could be expected that more connection between turn angle and displacement could be seen.

There was large variation between individuals for size of home range, use of the home range, and occupation level. For the same three month period, the size of the home range varied from 49 km^2 to 879 km^2. Large variations in home range sizes are also seen in the literature, for example (McCarthy et al., 2008) report home range sizes between 12 km^2 to 451 km^2. In these earlier publications, many of the substantially smaller home ranges were calculated using radio tags (McCarthy et al., 2005) and this may be biased by the difficulties of data collection rather than the actual size of snow leopard home ranges. In this study, the denning females with cubs tend to move less, which may explain some of the variation in the data (McCarthy and Johansson, 2013). Variation of this magnitude in home range size would have implications for the reliability of both CMR and SECR.

Analysis of the use of home ranges shows that, on average, snow leopards distribute their time equally over the whole of their home range. This does not match the assumptions in the original form of the SECR, and therefore it is interesting to see whether this will impact on the method's reliability for species like snow leopards, to be discussed in Chapter 4. Whilst this pattern is repeated for the average of all subpopulations, there is large variability within subpopulations. The occupancy levels of snow leopards again shows a similar pattern between subpopulations, with a positive skew implying a large variation within subpopulations.

3.4.3 Movement simulations

Simulations undertaken using the clustering models produced a more realistic distribution of displacement and turn angle than the random walk in the short term (locations separated by five hours). However, they do not produce the variety of movement patterns that are seen in snow leopards. Validation datasets show that in both the displacement and turn angle there is still a bimodal distribution after 25 hours. This implies that the movement of snow leopards is not just dependent on current behaviour, but each animal has memory for at least one day, or a spatial memory that implies that animals return to the same place. McCarthy et al. (2005), saw obvious evidence of this medium term memory when studying snow leopards in Mongolia, with animals returning to resting places that were previously used. Anecdotal evidence suggests that this is often a result of animals returning to a kill site (McCarthy and Johansson, 2013). Therefore a Markovain model does not represent the true system, and a model with this level of memory might be more appropriate. However there are other factors which were not modelled would also have an impact on the movement simulation, including, but not limited to: the energy landscape; the true distance travelled when including changes in altitude; locations of human settlements, and there impact on snow leopard behaviour.

The simulations from the cluster models produced values visually closer to the validation data than the random walk for both size of home range and occupancy levels. The cluster models created home ranges that were realistic; however, the simulations produce home range size and occupancy levels with low levels of

variation. Whereas, in reality, the variation in home range sizes and occupancy levels between individuals is much larger. The size of the home range, and occupancy levels, may affect the accuracy, or the precision, of density estimation models. Consequently, this feature of the simulation may affect the inference in later analysis.

3.5 Conclusion

One of the hypotheses was that types of movement would be visible from data, and these may relate to specific behaviours. To some extent this is true: resting behaviour, where animals do not travel for up to 25 hours, and traveling behaviour, are visible. However, the coarseness of the temporal spacing means that more detailed behaviours, such as sprinting, cannot be identified from this dataset. When using a clustering algorithm, the data are split into clusters that translate to fast forward movement, slow forward movement, and movement with a complete change in direction.

In the studies on other felid species, no noticeable differences between sex and season were observed (Sandell, 1989; Sollmann et al., 2011). In this population there were few significant differences between subpopulations. The most obvious difference was between the displacement in summer and winter seasons, but there was also a difference in displacement between sexes. These significant differences in displacement meant that modelling had to be done separately for males and females, based on only the summer data. However, none of the other parameters showed any significant differences by sex or season.

To some extent, the patterns found in the data were successfully replicated. Short term movement distributions were recreated using cluster-based models, as well as occupancy levels, and size, and use, of home range. However, medium to long term movement strategies were not replicated well under any of the models. The snow leopard movement does not appear to follow a Markov principle, as there appears to be more memory in the system. Therefore, when using clustering, there is no strong reason for choosing Markovian transitions, as this neither substantially improves the replication of movement patterns nor fits the underlying system better.

3.5.1 Further work

There are various ways that the model of movement could be improved. The models failed adequately to model long term patterns in movement. A multi-dimensional Markov chain might be appropriate for including memory of previous states; however, overfitting the model would be a concern for this dataset. For example, creating a cluster model using a 3-dimensional Markov transitions would have required 161 parameters to be calculated from 1393 locations, resulting in a ratio of data points to parameters of less than 10.

The model also fails to reproduce the variance in the data. Allowing the size of boundary and locations of clusters to be chosen from a distribution, rather than being a fixed value, may allow greater variation in the size home range, and the occupancy levels in individual animals. This may be an interesting area to explore in a sensitivity analysis, to see whether heterogeneous animal behaviour has an impact of optimal camera trapping strategies.

The main limitation of this movement analysis is the temporal spacing of the GPS fixes. If more data, and higher frequency of locations, had been available then more parameters would have been included in the models. These might include the time of day, the altitude, and the vegetation type, as these may highlight interesting ecological features that may be of use for researchers and conservationists. However, once again, the inclusion of more variables into these models could result in overfitting.

Chapter 4

An avalanche of data: How to optimise camera studies for snow leopards

Contents

4.1 Introduction

In order to manage a species well, and to evaluate whether conservation techniques are working, it is necessary to have a good understanding of the size of the population (Legg and Nagy, 2006; Yoccoz et al., 2001). Therefore, researchers are not only seeking an accurate estimate but an estimate at high precision, because without this it is impossible to tell whether there has been change in the size of the population (Rosenblatt et al., 2014). A simulation study by Efford and Fewster (2013) showed that spatially explicit capture recapture (SECR) had a higher level of accuracy than capture-mark-recapture (CMR), and reached what they considered to be an adequate level of precision, a relative bias of between 0% and 10%. Based on this, and the results in chapter 2, this section of the thesis concentrates on the SECR methodology.

The accuracy and precision of any model can be eroded if the data does not meet the assumptions being used. This may be a practical problem for many researchers using SECR because the analysis in chapter 3 shows that there can be substantial differences between realistic movement and SECR assumptions.

4.1.1 Introduction to SECR calculations

CMR has been used in ecology for a long time. It directly estimates abundance of the target species, which in turn can then be used to estimate density by dividing by

the estimated effective sampling area. One of the advantages of SECR methodology is that density is directly estimated, rather than relying on separate calculations. In theory this should make it a more reliable estimate (Borchers and Efford, 2008; Efford et al., 2009), as the methods for estimating effective sampling area are not reliable (Wilson and Anderson, 1985; Efford and Fewster, 2013).

Like CMR, SECR assumes that animals are always correctly identified, and that detections are independent. But SECR also includes assumptions about animal movement, so detectors have to be placed randomly with respect to the location of activity centres. In addition, SECR assumes that an animal has a centre to its home range, where it is most likely to be captured, and that the chance of capturing the animal reduces in a predictable manner with the distance to the centre of the home range. This decay in capture probability is assumed to be symmetrical around the centre of the home range, and is modelled by the detection function, $g(d)$. This detection function is normally based on two parameters g_0 and σ; however, coefficients can also be added to include additional parameters, for example the sex of the animal (Efford, 2015; Gray and Prum, 2012). The simpler models assume that the g_0 and σ values are the same across all individuals in the survey area. These coefficients are calculated by maximising the likelihood of the detection function parameters, density and home range locations, given the number of animals and their capture histories. The capture history for the i^{th} animal is $w_i = \{w_{i1} \dots w_{iS}\}$ where $w_{iS} = k$, where i is the animal, S is the occasion, and k is 1 if there is a capture and 0 if there is no capture.

In SECR, the centres of the home ranges are assumed to be randomly distributed. For many felid species this would be an unfair assumption as there is little to no overlap of individuals within the sexes as some species can be highly territorial. However Jackson and Ahlborn (1989) showed there is overlap between and within sexes for snow leopards. Therefore the assumption of randomly distributed home ranges is much more reasonable than for other species, and therefore was assumed in this analysis.

Previously, SECR has been tested with simulations to determine some of the conditions that cause bias. None of these simulations use an explicit model of animal movement: either capture matrices are generated based on the same assumptions that are used in the SECR model (Tobler and Powell, 2013; Royle et al., 2013a; Efford and Fewster, 2013), or the capture matrices are simulated based on a probabilistic model of their own design (Ivan et al., 2013). It should be noted that most the previous simulation studies rely on the underlying assumptions of movement to create the capture matrices. For example, Tobler and Powell (2013) used the assumptions of the SECR, that probability of capture is maximised at the centre of the home range and that this decreases with mathematical function given distance in their simulations. If the underlying assumptions of movement are not correct, and there is evidence to believe that they are not, then the conclusion of these studies may not be valid.

Tobler and Powell (2013) used the internal simulation the in the SECR package in R (Efford, 2011) to evaluate ideal survey areas for a Jaguar (*Panthera onca*) population with density between 1 animals$/100\text{km}^2$ - 4 animals$/100\text{km}^2$, and with home range area between $150\,\text{km}^2$ and $400\,\text{km}^2$. Tobler and Powell (2013) make a number of suggestions about ideal survey design for jaguars. But given their findings, they go on to suggested that the number of camera traps currently used in the field is not sufficient for calculating reliable density estimates and that 40-50 cameras should be used. Finally Tobler and Powell (2013) suggested that running the internal simulation in the SECR package in R would be good practice before designing a survey, since it would act as a check to whether the survey design would produce unbiased results. However, as the movement of some animals do not match the assumptions of the SECR, as shown by the snow leopard study in chapter 3, this internal simulation may not be an adequate guide as to optimal camera placement for SECR density estimation.

Ivan et al. (2013) ran a simulation study comparing different methods of calculating density, including CMR and SECR. Their simulation involved dividing the space into a series of blocks, randomly placing home ranges and assigning a capture

probabilities based on the overlap between study area and home range. If the probability of capture was large enough, the capture location was then assigned. The simulated density was much higher than in most felid studies, 40 000 animals/100km^2 - 160 000 animals/100km^2 (4 - 16 animals/ha), but Ivan et al. (2013) found that that SECR worked poorly when the home ranges were stretched out, rather than square or circular. This is because the assumptions of original SECR imply that home ranges should be symmetrical, and therefore σ could be overestimated if captures are made on the long-axis of the home range.

Other simulations used the underlying movement assumptions, including: Royle et al. (2013a) who used simulation to investigate their new model which takes into consideration the costs of traveling through different environments; and Efford and Fewster (2013) who showed that SECR has a lower bias level than non-spatial methods. Efford and Fewster (2013) also investigated the layout of cameras, and showing that rather than having one large block of cameras, it is possible to use multiple smaller blocks of cameras in SECR survey design without adverse affects, something that was not possible with CMR.

4.1.2 SECR and snow leopards

Snow leopards are a cryptic species, easily identifiable from photographs because of their pelage markings; however, to the best of my knowledge there has only been a single study (Alexander et al., 2015) that has published density estimates for snow leopards using SECR. There are a number of practical challenges when studying snow leopards, including: their extremely low density, their large home ranges, and the mountainous terrain in which they live (Alexander et al., 2015).

Alexander et al. (2015) ran a study on snow leopards in the Qilianshan mountain range in China. They used 60 cameras over 480 km^2, and this could be anywhere between 133% and 4400% of the average snow leopard range, based on home range estimates in Chapter 3 or Jackson (1996). Alexander et al. (2015) estimated density used SECR, with a half normal detection function (3.31 animals/100km^2) and an exponential detection function (3.51 animals/100km^2), but also compared their results with CMR (8.31 animals/100km^2) and occupancy studies. Once they

removed unidentifiable animals from their sample, they found 20 animals, most of which were only captured once, with only one animal being caught as many as seven times. The mean maximum distance moved between camera locations was reported as 7.60 km(SE = 4.16 km). Alexander et al. (2015) do state that the estimates of density in their study might be high because of the number of single captures they accumulate.

None of these problems are unique to snow leopards. In particular, the effect that low density populations have on the accuracy of the density estimates has been considered a number of times before. After replicating the simulations used in the original paper, Marques et al. (2011b) cast doubt on the ability of the SECR methodology to estimate density for sparse populations in their discussion paper. Tobler and Powell (2013) also ran a simulation study, and theorised that lower density species would require a larger survey area, which agreed with the Marques et al. (2011b) paper, in which it was suggested that the survey area could be a problem in low density species.

Researchers have created density estimates using SECR on other low density species. Royle et al. (2011) estimated the density of the wolverine (*Gulo gulo*) population using SECR at 0.97 animals$/100\text{km}^2$. However, as in other studies, because a ground truth value is not known, it is not possible to evaluate the estimate for accuracy. In addition to this, Weingarth et al. (2015) preformed a SECR study on lynx (*Lynx lynx*), a medium-sized cat which also occurs at low density. They reported difficultly in balancing the demographic closure requirement (no births/deaths) with the minimum number of captures requirement due to the low capture rate. In order to achieve a 75% chance of obtaining 20 captures, a study would need to be run for at least 80 days, and between 100 and 120 days for a better estimate.

4.1.3 Summary of the guidelines

There are two points at which a researcher can easily change the reliability of the study: the first when they design the survey, and the second after they collect the data when they apply a model to the results. There are two sets of guidelines which reflect this.

- The first governs how a study should be designed. If the final intention is to use a SECR model, then the survey area must be larger than the standard home range, and the distance between cameras should be smaller than the radius of the home range. There is also an assumption of demographic closure, so researchers have to identify a suitable time period in order to minimise inevitable changes in populations (Sollmann et al., 2012b; Tobler and Powell, 2013).

- The second set of guidelines is what the photographic record should look like if the SECR model is going to be applied. The only guideline that exists is that there should be at least 20 captures, and that 10 individuals are needed if sex coefficients are to be included. There are no guidelines covering the distribution of these captures, but at least one animal should be captured at multiple cameras, otherwise the SECR does not converge. This is because the model cannot estimate σ without some evidence of the possible home range; therefore it follows that the estimate for σ would be improved if animals were collected on a large proportion of locations in their home range.

4.1.4 Aims and hypothesis of chapter

This chapter tests whether SECR provides an appropriate measure of density given the difference between the assumptions of the underlying detection functions and the movement of animals in the wild. This chapter tests whether if some of the movement assumptions in SECR are invalid the density estimates produced will be biased, and in what direction. There are a number of variables that are not considered in the movement simulation and therefore even if the SECR methodology stands up to this analysis, this does not mean that it would be robust in the field. In addition, this chapter explores how much effort is required for an accurate and precise estimate, and what restrictions there are on survey designs and capture matrices. There are a number of serious practical difficulties that make a robust examination of these properties impossible in the field, so this was done using simulation techniques. The parameters in the simulation were matched as closely as possible to the

parameters in the real world. Unlike previous simulations studies, this thesis uses an explicit model of movement, based on the model of real animal tracking data developed in chapter 5. This replicates important aspects of each animal such as speed, path tortuosity, and the size and use of the home range.

This chapter will address the following questions:

- Does the SECR methodology work when some of the movement assumptions are invalid? Such that, in the limit, when many cameras are used over a large area, the average bias on the density estimate will be zero
- Is it possible to get an unbiased density estimate using SECR when "normal" camera numbers are used? Where average camera numbers are taken from chapter 2, and range between 25 and 42 cameras
- Do the survey area and inter-trap distance guidelines discussed in chapter 2 produce unbiased density estimates?
- Will a larger number of captures result in a less biased result?
- Is the distribution of the captures, over area and individuals, important to the bias of the result
- Will the internal simulation in the SECR package in R, and snow leopard simulation generated in this thesis, produce significantly different density estimates to each other, even when parameters are matched as closely as possible

4.2 Method

This section describes how the simulation studies were designed, and the process of matching parameters to behaviour that is seen in the real world. It then moves on to describe the analyses that were performed on the simulation results.

4.2.1 Simulations

The simulation world was set-up such that there was a grid of 100 by 100 cameras, separated by 1 km, surrounded by a buffer region of 2 home range radii. This world

was randomly populated with snow leopards at a given density. Random placement was thought to be appropriate because overlapping occurs between and within sexes (Jackson and Ahlborn, 1989). There is a difference between random and overlapping, the locations of home range centres in reality are based on a large number of factors, many of which are not included in the simulation, and many of which are not known. As no other strategy has been suggested for snow leopards, random placement would be a conservative assumption. The animals started at the centre of their home ranges, but the run-in period of 30 days was used so that individuals were not necessarily at the centre of their home range when the cameras were running. After this run-in period, the movement continued for two months, where the captures were collected when an animal moves through the given camera detection zone. This two month sampling period was based on the average length of surveys calculated in chapter 2 (Table B.1). The sampling period is not extended because, in the real world, it is important that the assumption of demographic closure is met. The capture matrices were formed based on a sampling occasion of 5 days, so that 12 sampling occasions were used in total. The simulation was coded in C++, and was replicated 1000 times.

4.2.1.1 Settings simulation parameters

The parameters that are matched to the real world include: the density of snow leopards, the capture rate of snow leopards, and the movement of snow leopards. The literature was surveyed to find estimates for the density and capture rates of snow leopards (Table C.1). The density estimation of snow leopard recorded in the literature are positively skewed, with a mean value three times the size of the median value (Figure 4.1). As the data are so heavily skewed, the density of snow leopards used in the simulation is based on the median density estimate, approximately $0.8\,\text{animals}/100\text{km}^2$.

The capture rate in the literature was also positively skewed, so again the median capture rate was chosen, approximately $0.56\,\text{captures}/100\text{day}$ (Figure 4.2). Due to the camera placement and the independence of snow leopard movement, the capture rate in the simulation is much lower than would be seen in reality. The ra-

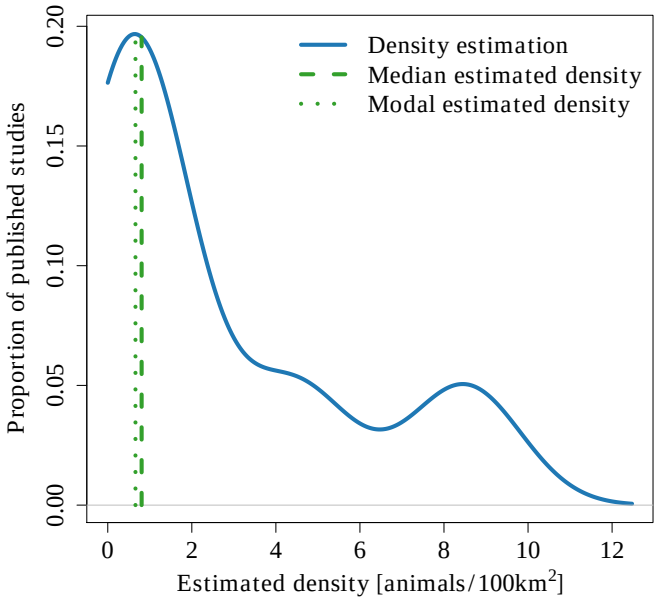


Figure 4.1: The distribution of density estimates found in the snow leopard literature. The mean, median and modal density estimations found in the literature are 2.57 animals/100km^2, 0.81 animals/100km^2, and 0.67 animals/100km^2 respectively

dius of the camera was varied until the capture rate in the simulation was raised to the level seen in field surveys. This was based on the assumption that any animal that passed within a given distance of the camera would be likely to be funnelled to the camera location by a combination of topography or camera placement. Multiple sets of simulations were run to set the ideal camera radius (Figure 4.3), and, for this simulation, the camera radius was set to 55 m.

The movement parameters that were calculated in chapter 3 can be found in Tables B.11 - B.18.

4.2.2 Testing behaviour in the limit

The first analysis used the capture data from all 10,000 cameras in the simulation. This would represent a very large, very dense, grid of cameras that would be highly unlikely, if not impossible, to place in reality. If this analysis produces a biased result, then we could question whether SECR would be a viable method with any level of effort.

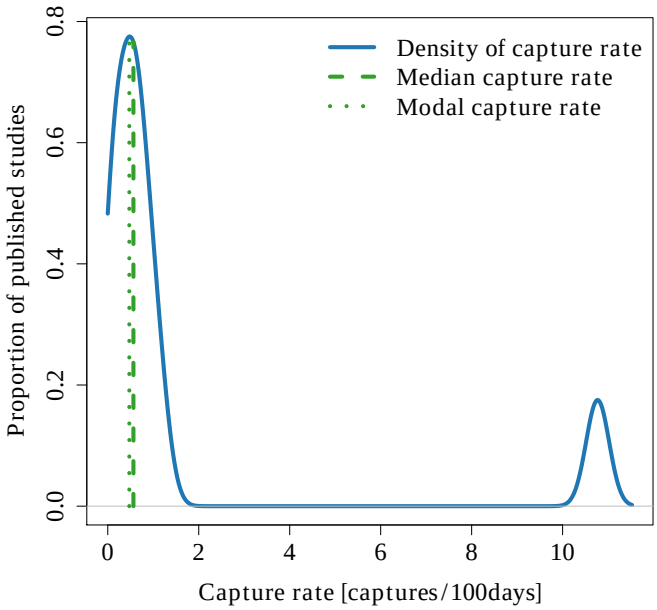


Figure 4.2: The distribution of capture rate for snow leopard when using camera traps, measured in number of captures per 100 days of camera time, the median value and modal value were 1.65 captures/100day, 0.56 captures/100day and 0.47 captures/100day respectively

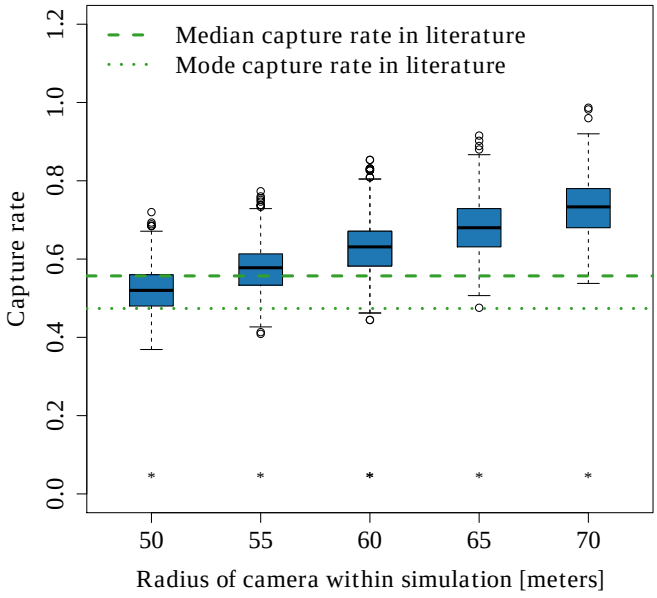


Figure 4.3: The distribution of capture rate for a range of camera radii within the simulation

Two detection functions were used to calculate the density in the SECR package in R (Efford, 2015): the half normal, and the w-exponential. The half normal detection function is the most commonly used default function, where the half-normal detection function is given in equation 4.1.

$$g(d) = g_0 \times exp\left\{\frac{-d^2}{2\sigma^2}\right\} \tag{4.1}$$

Where d is the distance from the centre of the home range, g_0 is the capture probability at the centre of the home range and σ is the rate of decrease of capture probability.

The half normal detection function assumes that the movement falls off at a gradual rate from the centre of the home range; however, the analysis in chapter 3 shows that this is not a valid assumption for snow leopard movement. Other detection functions may be a better fit to the data, for example, the w-exponential detection remains constant for a distance w around the centre of the home range, then falls off with an exponential pattern (Efford, 2015). This is a highly flexible function and can allow either large areas with constant g_0, or small areas, with rapid fall off. The w-exponential detection function, is given in equation 4.2.

$$g(d) = \begin{cases} g_0 & \text{if d} < \text{w} \\ g_0 \times exp\{-(d-w)/\sigma\} & \text{if d} >= \text{w} \end{cases} \tag{4.2}$$

Where d and w are distances from the centre of the home range, g_0 is the capture probability at the centre of the home range and σ is the rate of decrease of capture probability.

The bias in density for both detection functions was tested using a t-test, to test whether the median bias significantly differed from zero, and the results were plotted using a boxplot.

4.2.3 Realistic camera numbers

From the analysis that was performed in chapter 2, it is known that the average number of cameras in a felid survey is either 26 cameras (median) or 43 cameras

(mean) (Table B.1). In order to run analyses using more realistic camera numbers, the large camera grid was subsampled so that five different effort levels could be studied:

- 25 cameras (5 by 5 grid),
- 30 cameras (5 by 6 grid),
- 36 cameras (6 by 6 grid),
- 42 cameras (6 by 7 grid),
- 100 cameras (10 by 10 grid)

Each of these effort levels was studied, with variation in different inter-trap distances, The distance varied varied between 1 km and 15 km; (the 100 camera effort level was studied with inter-trap distances ranging between 1 km and 10 km). The captures from these subsampled datasets were turned into capture matrices, where each sampling occasion was 5 days long.

The density was calculated using SECR with a half-normal detection function, the default detection function. The bias in density for each survey design was tested using the Wilcoxon test to see whether the median bias significantly differed from zero. The Wilcoxon test was used as the data may not be normally distributed. As multiple tests were done of the different inter-trap distances, adjustments were made for multiple testing done using the Bonferroni correction. For each effort level, the distribution of bias for each survey design was plotted using a boxplot.

The effect that effort has on accuracy and precision were shown in two separate graphs. Firstly, accuracy was shown by plotting the median bias of density estimates by survey areas, for 25 cameras, 30 cameras, 36 cameras, 42 cameras, and 100 cameras, on the same graph. Secondly, the effect on precision was shown by plotting coefficient of variation for each effort level by survey area.

4.2.3.1 Causes of bias

Biases are present in some of the survey designs. In order to explain why these biases arise, this section looks at the estimation of the internal parameters, g_0 and

σ. These were plotted against survey area, to identify patterns of overestimation or underestimation that might occur, and compared to the values of g_0 and σ estimated when 10,000 cameras were used.

In addition, the structure of the captures may be important for the estimation of g_0, σ and density, and, therefore, additional variables were collected that might explain the bias in estimates. These included: the number of captures, and the percentage of animals captured, the number of cameras at which an animal is captured, the percentage of recaptures, and the distance between recaptures. This was calculated in two ways:

- The average maximum distance between the captures. For example in figure 4.4 is $\frac{(D1+D2+D3)}{3}$
- The maximum distance between the recaptures. For example in figure 4.4 is D3

As the capture rate has been set in the simulation, it should be expected that the number of captures will remain close between simulations. However, the other variables are expected to change as the survey area changes. These patterns were shown using boxplots. These values may also impact the estimate of g_0, σ and density, therefore correlation tests were run between each variable and these three outcomes. Running regression models on these variables would not be appropriate due to the autocorrelation in the variables, lack of homoscedasticity, and non-Gaussian distributions.

Finally, using these variables, a new guideline was produced by identifying the variables that correlated best with the g_0, σ, and density to find a better guideline for density estimates using the SECR. This guideline was then tested on a new sample of simulations.

4.2.4 Comparison of simulation methods

Additional internal simulations were run to assess whether the movement generated through the internal simulation, and the simulation of snow leopard movement produced earlier, results in similar biases in the SECR. The parameters used in these

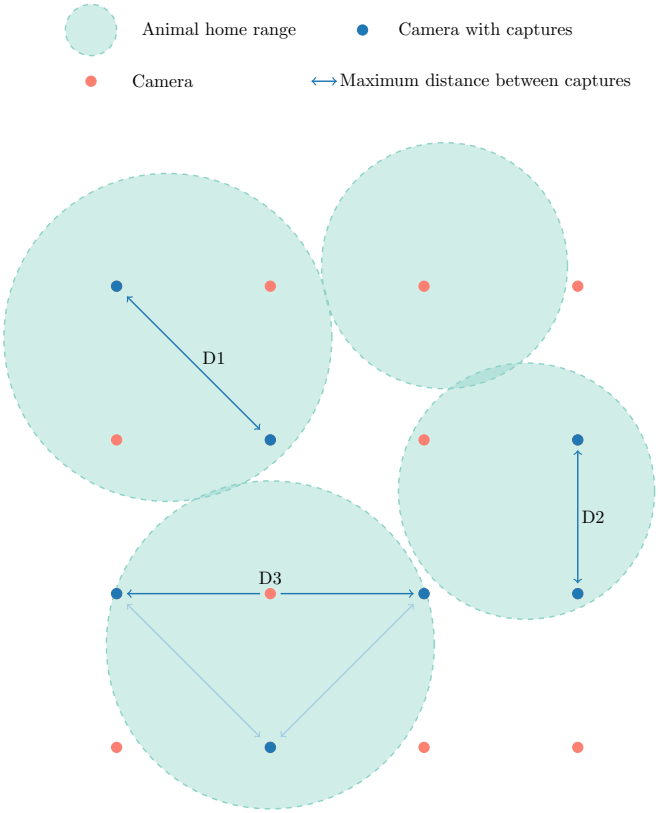


Figure 4.4: Diagram showing the distance calculations for variables

simulations were equal to the median internal parameters values (g_0, σ) in the analysis of 10,000 cameras, and the internal simulation used a half-normal detection function. In order to match realistic surveys, the simulations contained 25 cameras (5 by 5 grid), and 42 cameras (6 by 7 grid), for which inter-trap distance varied from 1 km to 15 km.

To compare the results based on the different simulation methods they were plotted on the same graph with the medium value represented by a bold line, and the middle 50% shown as a shaded region. The precision of the two methods was also considered, with the coefficient of variation plot by survey area and simulation type.

4.3 Results

The results section starts with an examination of two detection functions, and what occurs when a large surveying effort is used. This examination is important to make

sure that, when a large number of cameras is used, the methodology is applicable to species whose movement patterns may differ from the assumptions of SECR. It is not always possible to deploy a large number of cameras. Consequently, subsequent analyses employed a more realistic number of cameras. By examining the bias at each effort level, this chapter estimates the minimum amount of effort required to set up a successful field survey.

If researchers use the internal simulation in the R package to test survey designs before deployment, then it is important that they know whether the underlying assumptions that produce estimates of accuracy and precision are realistic. Therefore, this chapter also examines the differences between results from the internal simulations and the simulation created in chapter 3. If the two methods produce similar results, then using the internal simulation to evaluate a possible field survey would give an idea of the level of bias the design might generate. However, if they do not produce similar results, then using the internal simulation may not be a suitable method for evaluation of field survey designs.

Finally, this chapter looks at whether the distribution of captures over individuals and area impacts the estimation of the internal parameters, and therefore the accuracy and precision of the density estimate. This is important to see whether the guidelines for producing density estimates could be improved.

4.3.1 Invalid assumptions affect the limit

Using a large number of cameras with the default half-normal detection function, the average bias in the density estimated produced using SECR is not significantly different from zero (figure 4.5). Therefore SECR does work in the limit, even when the movement assumptions and independent capture assumptions are broken. The density is estimated as $0.79\,\text{animals}/100\text{km}^2$ (95%: $0.77\,\text{animals}/100\text{km}^2$, $0.80\,\text{animals}/100\text{km}^2$); however, even with a large amount of effort, the true density is at the edge of the 95% interval (p = 0.06). This simulation produced average internal values: $g_0 = 0.0224$ and a $\sigma = 5594$ metres, which were used later as the inputs for the internal simulation and as a comparison for the g_0 and σ values in other simulations.

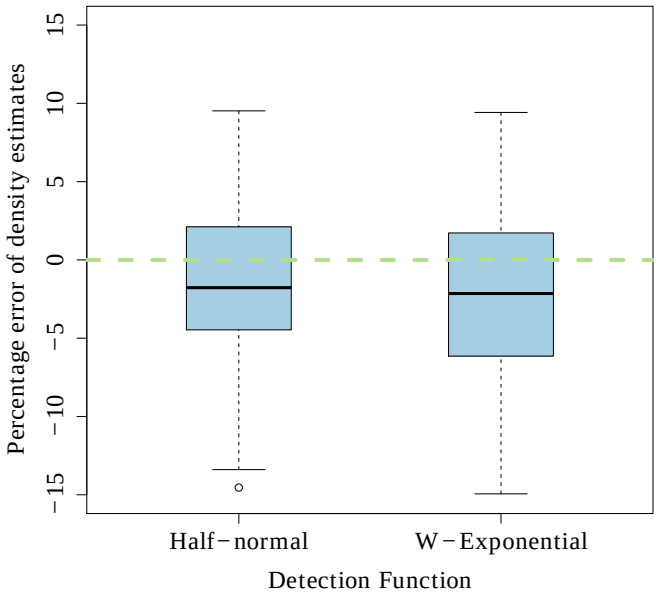


Figure 4.5: The percentage error of densities estimated using SECR, when 10,000 cameras are used. Where the black line represents the median percentage error across all simulations, boxes represent the middle 50% of the data, whiskers represent variability outside the upper and lower quartiles with outliers plotted as individual points.

When a w-exponential detection function was used, it is resulted in a median density of 0.78 animals/100km^2 (95%: 0.77 animals/100km^2, 0.79 animals/100km^2), and produced average internal parameters of: g_0 = 0.06 , w = 10 metres, and σ = 3423 metres. When using the this detection function, the density estimate significantly differs from the true density value in the simulation (p = 0.003), showing that it is not an appropriate model for estimating density. The internal parameters suggest that the probability of capture falls off quickly around the centre of the home range, rather than having a large area where probability of capture is constant as the movement model suggests. The estimated value of w is much smaller than what would be expected given the analysis in the simulation. This may be due to the fact that the movement model does not specify how the home range should be used, and therefore each individual in the simulation uses the space differently.

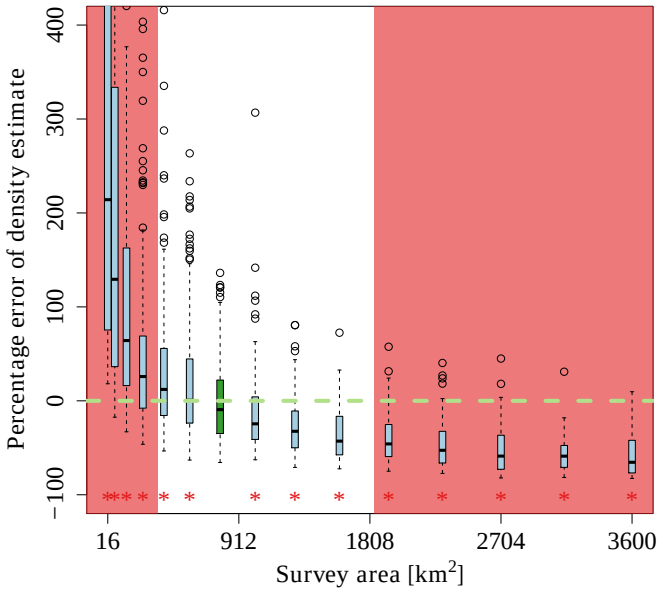
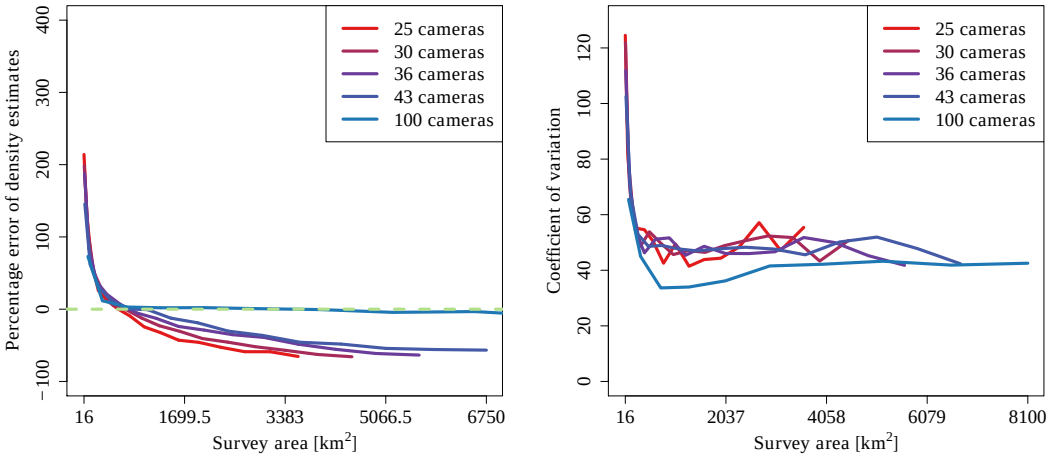


Figure 4.6: The percentage error of densities estimated using SECR, when 25 cameras were used, with inter-trap distances ranging from 1 km to 15 km. The average home range size for each animal was kept as constant at 360 km. The boxplots in the red area are biased due to small survey areas, or because the camera spacing is too wide (if the guidelines discussed in chapter 2 are correct). A green boxplot with a red stars indicate that the median of the box is significantly different from 0 percentage error.

4.3.2 Realistic camera numbers

The average number of camera traps typically used in density estimation research on felids is between 26 cameras and 43 cameras (Table B.1). Therefore, this chapter, considers survey designs with between 25 cameras and 42 cameras. The outcomes with these varying amounts of effort were compared to the guidelines in chapter 2. This showed that the simulations were biased in the areas where the guidelines suggest there would be biases; however, the guidelines do not cover all the non-biased camera layouts (Figure 4.6, and Figures C.2a - C.3b). All of the simulations showed the same pattern; they overestimate the density at low survey areas, and underestimate the density as the survey area increases (Figure 4.6, and Figures C.2a - C.3b). This pattern has been seen before in other simulation studies (Tobler and Powell, 2013).



(a) Accuracy **(b)** Precision

Figure 4.7: The accuracy and precision given the amount of effort included in the survey, showing a) the median percentage error and b) the coefficient of variation of densities estimated using SECR, when differing efforts were used, with inter-trap distances ranging from 1 km to 15 km. The average home range size for each animal was kept at 360 km. Dark blue represents 25 cameras, light blue represents 30 cameras, yellow represents 36 cameras, light green represents 43 cameras and dark green represents 100 cameras respectively.

The optimal survey design for each effort level falls in the range suggested by the layout guidelines. However, significant biases, result even if the guidelines are followed properly.

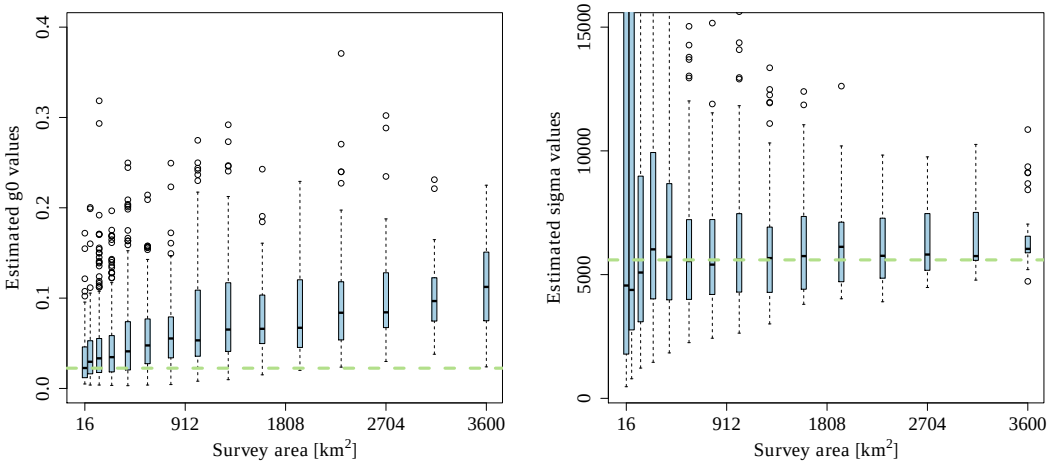
In general, as the number of cameras used in a survey gets larger, the SECR methodology is less sensitive to the survey design, as the average bias reduces for a fixed survey area, and more survey designs will produce unbiased estimates if the researcher has more cameras to deploy (Figure 4.7a). When 25 cameras are used then the unbiased estimates are only possible when the inter-trap distance is between 6 km and 7 km (Figure 4.6, and Figure C.1) and, when 42 cameras are used, the inter-trap distance needs to be between 5 km and 6 km for accurate estimates (Figure C.3a). When effort is available to increase deployment to 100 cameras (an unrealistically large number of cameras), the number of unbiased survey designs increases dramatically, such that estimates are approximately unbiased when the inter-trap distance is between 3 km and 9 km (Figure C.3b).

The effect of increasing effort on precision is less obvious than the effect that increasing effort has on the accuracy of the density estimate. Whilst the precision also increases as the effort increases (Figure 4.7b), there is little difference between 25 cameras and 42 cameras and only once there is 100 cameras is there a substantial increase in precision. The precision peaks between 730 km and 2025 km, approximately between 2 and 5 times the size of the average home range. If the survey area is too large or too small then the precision of the estimate decreases.

4.3.3 Causes of bias

This last section of results deals with why the over- and under-estimation of the density may be occurring, this is done by also considering the internal parameters of the SECR, g_0 and σ. These two internal parameters, if miscalculated, can cause error in the density estimate. When the survey area is small, g_0 is estimated well, but, as survey area and inter-trap distance increase, the SECR model overestimates the g_0 value (Figure 4.8b). This overestimation of g_0 would result in underestimation of density because it would assume that animals are more likely to be captured than is the case and, therefore, that a larger proportion of animals is captured than is the case in reality. The SECR model underestimates σ at low survey areas (Figure 4.8a); this would lead to an overestimate in animal density as it results in effective sampling area being too small. At very large survey areas, the σ value is slightly overestimated, which may lead to some underestimation of density.

The number of captures is the traditional way of estimating whether an estimate would be biased (Sollmann et al., 2012b; Efford et al., 2009), with the guidelines saying that more than 20 captures is needed for a good estimate. However, the results here show that fewer than the 20 captures can generate a reliable estimate of density (Figure 4.9a), and over 20 captures does not guarantee a reliable estimate of density (Figure C.7a). More captures did not necessarily result in a better density estimate; it does however, strongly correlate with a larger estimate. This is because there is a significant negative correlation between the g_0 estimate and the number of captures. When the number of captures increases, the estimation of g_0 becomes more realistic. Dependent on survey design, this correlation varies between weak

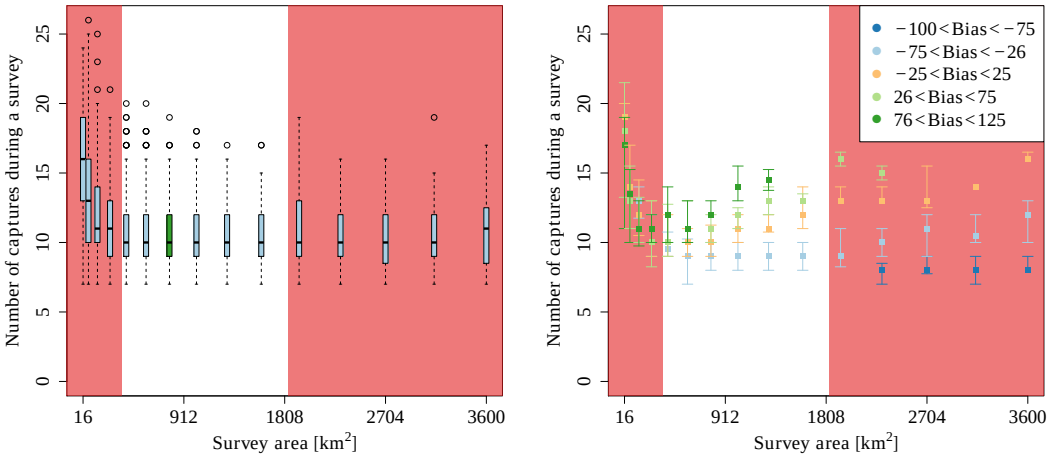


(a) g_0 **(b)** σ

Figure 4.8: The internal parameters from the SECR model, when 25 cameras were used, with inter-trap distances ranging from 1 km to 15 km. The average home range size for each animal was kept constant at 360 km. Where in plot a) the estimated g_0 values b) the estimated σ values.

and moderate; for example, between -0.10 and -0.58. g_0 gets smaller as the number of captures increases and this leads to bigger estimates. However, this only occurs when the area covered by the cameras is greater than 1000 km^2, approximately 3 times the size of a snow leopard's home range (McCarthy et al., 2008). The number of captures does not correlate with σ estimation, so increasing captures on its own will not reduce error from underestimation of σ (Table C.2 - C.3).

The numbers of cameras on which an animal is captured, as measured by the maximum number of cameras per animal or mean number of cameras per animal in each simulation, reduces as the inter-trap distance increases (Figure 4.10a). An increase in the mean number of cameras per animal is strongly correlated with a decrease in density estimates, so as animals are captured on more cameras, the density estimate reduces. There is only weak correlation between the mean number of cameras on which each animal is captured and the estimation of g_0, and only then with small survey areas. So the density value is influenced through the σ estimation, and there is a moderately positive correlation between the mean number of cameras per animal and the estimation of σ. As σ increases, so does the effective survey



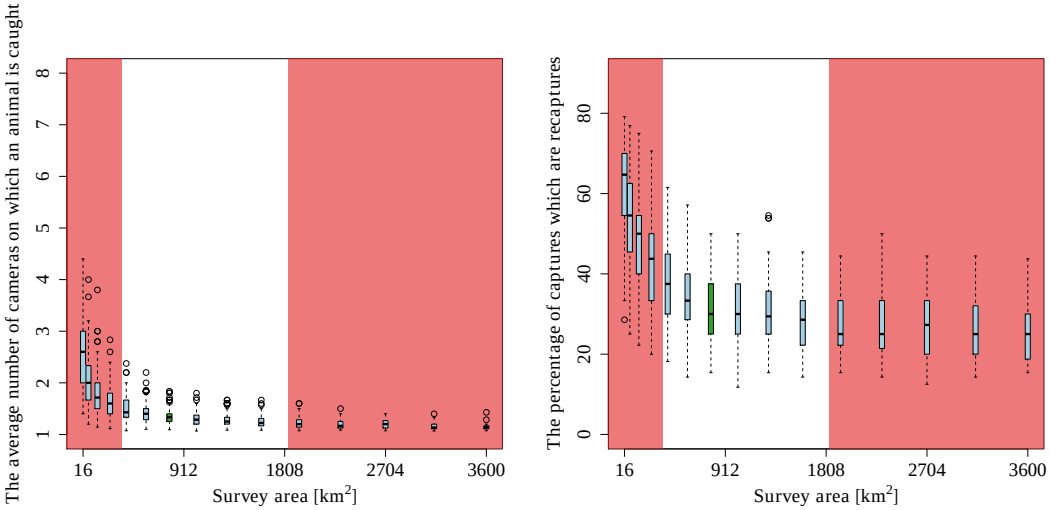
(a) Change in number of captures with change in survey design

(b) Change in percentage of animals captured with change in survey design

Figure 4.9: The change in collected data when 25 cameras were used in different survey designs, with inter-trap distances ranging from 1 km to 15 km. In plot a) the y-axis shows the number of captures, and in plot b) the y-axis shows the number of captures by the level of bias with blue points representing negative bias, green points positive bias, and yellow points being bias close to zero. Box plots, and points, in the red area should be biased due to small survey areas or wide inter-trap distances (based on the guidelines discussed in chapter 2). A green box plot shows that the median bias was not significantly different to zero, and a light blue box plot shows that the median density bias was significantly different from zero.

area, leading to a lower estimate. Therefore, an increase in the number of cameras an animal visits will decrease the amount of underestimation shown in the σ value for small survey areas (Tables C.4-C.7). On all of these measures, the average number of cameras on which an animal is captured is more strongly correlated with both σ than the maximum number of cameras. This implies that the capture of multiple animals on multiple cameras is important.

The percentage of recaptures falls as the area of the survey increases (Figure 4.11b). The percentage of recaptures is strongly correlated with the density estimate; as the percentage of recaptures falls, the density estimate increases, which is a result of the weak to moderate positive correlation between the percentage of recaptures and the estimated g_0 value. This is logical as the model assumes that all animals have equal probability of capture at the centre of their home range; if



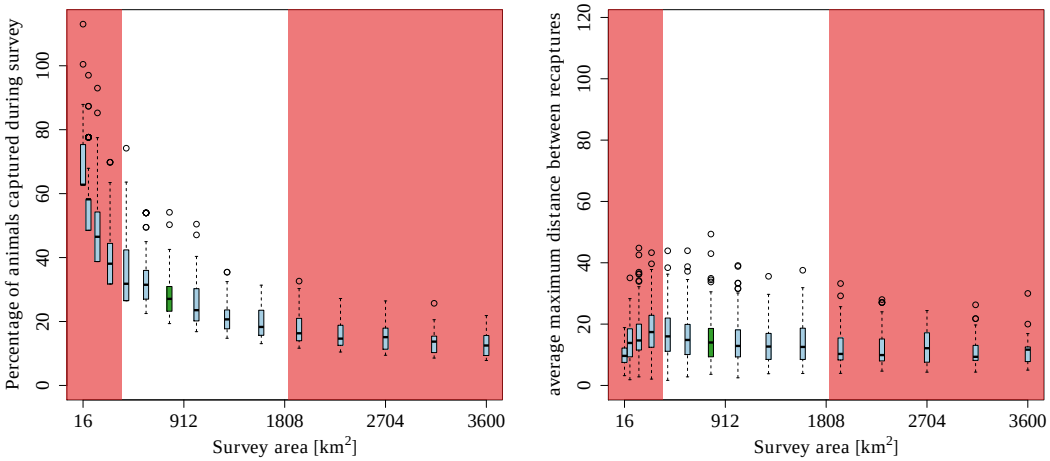
(a) Change in the mean number of cameras an animal visits with variation in survey design

(b) Change in percentage of captures with variation in survey design

Figure 4.10: The change in collected data when 25 cameras were used in different survey designs, with inter-trap distances ranging from 1 km to 15 km. In plot a) the y-axis shows the mean number of cameras any one animal visits, and in plot b) the y-axis shows the percentage of captures that were recaptures. Based on the guidelines discussed in chapter 2, box plots in the red area should be biased due to small survey areas or wide inter-trap distances. A green box plot shows that the median bias was not significantly different to zero, and a light blue box plot shows that the median density bias was significantly different from zero.

some animals are being recaptured often then it assumes there is a high probability of recapture in general, and therefore assumes that a larger proportion of animals have been captured than is the case in reality. There is, however, no significant correlation between the number of recaptures and the estimation of σ (Tables C.8 - C.9).

The percentage of animals that are captured reduces as the survey area increases (Figure 4.11b), and there is a strong correlation between the percentage of animals captured and the density estimate: as the percentage of animals increases so does the estimate of density. This is derived from the weak to moderately negative correlation between the estimated value of g_0 and the percentage of animals captured. As g_0 is overestimated in many of the survey designs, capturing more



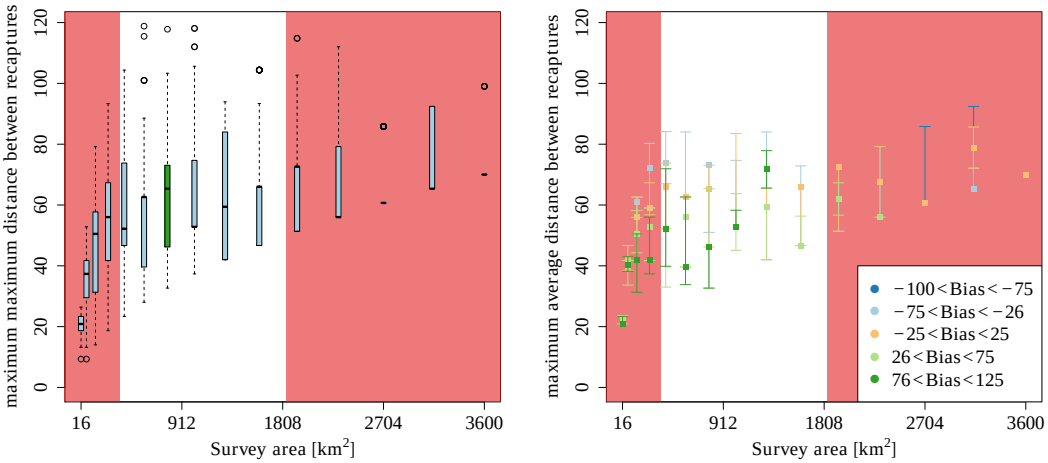
(a) Change in percentage of animals captured with change in survey design

(b) The average maximum distance between the captures

Figure 4.11: The change in collected data when 25 cameras were used in different survey designs, with inter-trap distances ranging from 1 km to 15 km. Where in plot a) the y-axis shows the percentage of animals that were captured, and in plot b) the y-axis shows the average maximum distance between the captures. Where based on the guidelines discussed in chapter 1 2, box plots in the red area should be biased due to small survey areas or wide inter-trap distances, and where a green box plot shows that the median bias was not significantly different to zero, and a light blue box plot shows that the median density bias was significantly different from zero.

animals would result in a better estimate of g_0. The percentage of animals captured is not significantly related to the estimated value of σ (Tables C.10 - C.11).

The distance between recaptures, as measured by distance 1 and distance 2 metrics, are both related to the survey area; however, this is not a simple correlation. The mean distance between captures is strongly related to the density estimation, whereas the maximum distance between recaptures is only significantly related when the survey area is small. As the distance between the captures increases, there is a reduction in density estimates. Both mean and maximum distance between recaptures are strongly correlated with both g_0 and σ. A strong relationship between σ and the distance between recapture is very logical, as the greater distance between recaptures implies a larger possible home range, and therefore a larger σ is estimated (Tables C.14 - C.15).

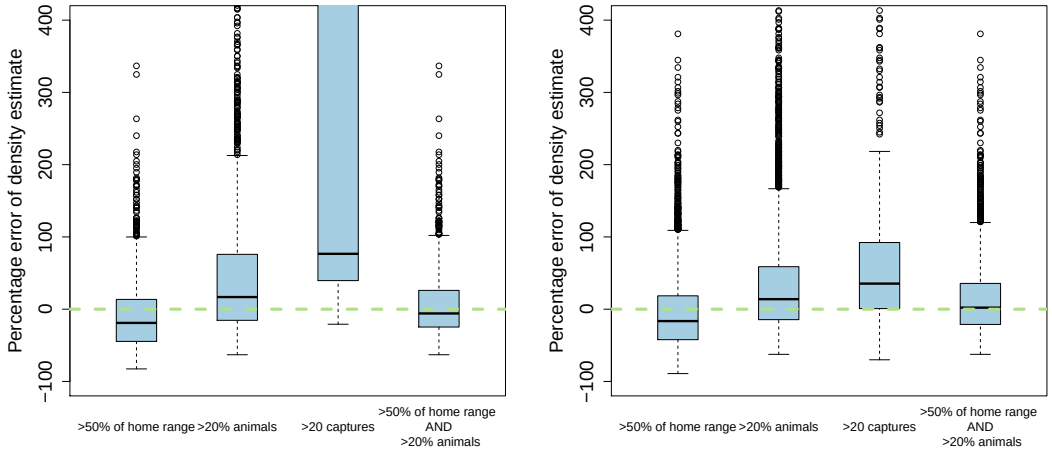


(a) The maximum distance between the recaptures

(b) The maximum distance between the recaptures, shown by by level of bias

Figure 4.12: The change in collected data when 25 cameras were used in different survey designs, with inter-trap distances ranging from 1 km to 15 km. In plot a) the y-axis shows the maximum distance between recaptures, and in plot b) the y-axis shows the maximum distance between recaptures by the level of bias with blue points representing negative bias, green points positive bias, and yellow points being bias close to zero. Based on the guidelines discussed in chapter 2, box plots in the red area should be biased due to small survey areas or wide inter-trap distances. A green box plot shows that the median bias was not significantly different to zero, and a light blue box plot shows that the median density bias was significantly different from zero.

Based on the correlation between the outputs and the density, g_0, and σ, the best possible estimate would have a large number of animals and at least one animal sampled over a large proportion of its home range. Therefore, rather than considering the number of captures, using a combination of the distance between captures and the percentage of animals caught creates a better guideline for a reliable estimate when low effort is applied. When considerable effort is applied there is little difference between the two measures. Collecting more than 20 captures is the least well performing guideline. Rather than aiming for more captures, a better aim is to capture more individuals (at least 20% in the survey area), and capture at least one individual across 50% of its home range. However this is not possible to guarantee this though survey design, and there would have to be some post-hoc evaluation of the data sample to see whether it fulfils this criteria.



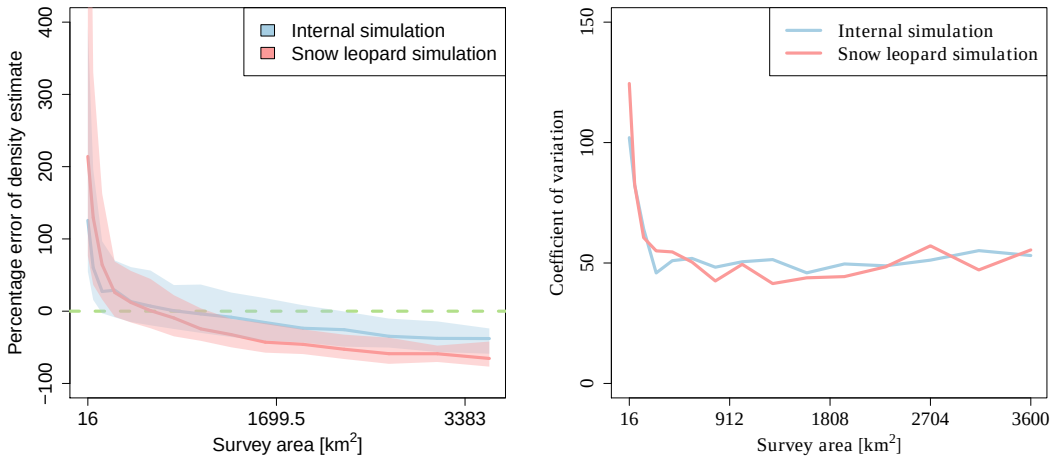
(a) The percentage error when simulations using 26 cameras pass various guidelines. The black line represents the median percentage error across all simulations, boxes represent the middle 50% of the data, whiskers represent variability outside the upper and lower quartiles with outliers plotted as individual points.

(b) The percentage error when simulations using 43 cameras pass various guidelines. The black line represents the median percentage error across all simulations, boxes represent the middle 50% of the data, whiskers represent variability outside the upper and lower quartiles with outliers plotted as individual points.

Figure 4.13: The percentage error for simulation when they pass certain guidelines, including capturing an animal across 50% of its home range, capturing at least 20% of the population, getting at least 20 captures, or capturing one animal across 50% of its home range and capturing at least 20% of the population. This was performed on a) 26 and b) 43 cameras

4.3.4 Comparison of simulation methods

Other researchers have suggested running the internal simulation in the R SECR package (Efford, 2015) to estimate whether the survey design they are planning to use would produce an unbiased estimate. In order to know whether the internal SECR simulation from the R package produced similar results to a explicit model of movement, both were run on the same survey design and effort. If a researcher were to use the internal simulation in R to estimate the accuracy of their survey design, they would achieve a lower indication of bias than if they had used the explicit simulation of movement. This effect becomes more pronounced when more effort is used (Figure 4.14a, and Figure C.4a). As the internal simulation is less biased than the explicit simulation of snow leopards, one might conclude, that re-



(a) Accuracy **(b)** Precision

Figure 4.14: The a) accuracy and b) precision of the SECR density estimate when 25 were used, with inter-trap distances ranging from 1 km to 15 km and 1 km to 10 km respectively. The average home range size for each animal was kept as constant between each set of simulations, 360 km. Where light blue, and pink represent the capture matrices calculated through the internal simulation and the snow leopard simulation respectively.

searchers who planned on testing their survey designs on the internal model may incorrectly evaluate their survey designs. However it is interesting to note that the precision of the density estimates does not substantially differ between simulation methodologies (Figure 4.14b, and C.4b).

4.4 Discussion

The purpose of this chapter was to analyse whether it is possible to estimate density correctly, within the limits of the model, using the SECR when the assumptions about movement were not met. It also aimed to explain why any biases might occur, and, therefore, what researchers could do to avoid bias. By proving that it is possible to obtain an unbiased estimate in the limit, when many cameras are used, the results show that SECR is a suitable method of density estimation. Given that it has identified that SECR is a suitable method for calculating density, the next step is to identify how much effort a researcher needs to apply to obtain an unbiased, and precise, result. An unbiased estimate can be produced when average

effort is applied; however, the design of the survey is very important. If the cameras are packed too tightly, then the density will be an overestimate as the internal σ value will be too low; and if the cameras are too widely spaced, the density will be underestimated as the internal g_0 value will be too high. All of the parameters that were considered either correlated with one or both of the internal g_0 and σ values, but, by ensuring a large proportion of the animals are caught and that the distance between captures for least one animal is greater than the radius of its home range, an unbiased estimate can be produced.

Researchers understandably want to check their whether their survey design will produce unbiased results before entering the field; the internal simulation in the R SECR package has been suggested as a suitable methodology. However if, like the snow leopards in this study, the movement of the target species does not follow the same pattern as is assumed in the detection function, using the internal simulation may create false confidence in the survey design. This chapter showed that when the same survey design and effort was used, the internal model showed less bias than the simulation of snow leopard movement, which is based on real movement data. Even if the simulation of the snow leopard is not an accurate representation, this analysis shows that if movement differs from the internal assumptions it has a substantial impact on the bias. Therefore, it is important for researchers to understand the movement of their target species.

This simulation here is not the ideal way of evaluating survey design, but as performing field surveys to generate the same standard would be near impossible, this represents one of the more tractable methods of studying the issue. In this simulation, the cameras and the animal movement are independent and, even though the capture rate was raised to a more reasonable level, the structure of captures may not reflect what is seen in the wild. The capture rate was highest when the inter-trap distance was small. This shows that, when the cameras are too close together, animals caught on one camera are more likely to be caught on a neighbouring camera soon after. This results in the breaking of the assumption of independent captures, an issue that could be a problem in the field.

4.4.1 Error in density estimation when using unrealistically large camera numbers

Whilst SECR does work with realistic movement patterns when many cameras are used along with the default detection function, the true density was on the edge of the 95% confidence interval for the half normal detection function, and just outside the 95% confidence interval for the w-exponential detection function. This might lead researchers to consider that, even at the limit, the SECR might underestimate slightly. It is important to note, however, that, as well as an invalid movement assumption, the assumption of independent detections is also broken when the cameras are close together: a capture in one camera would significantly increase the probability of the recapture being in one of the surrounding cameras.

4.4.2 Realistic camera numbers

The average number of cameras used in a camera trapping study is between 26 or 43 (Table B.1), as calculated from the data collected in chapter 2. There is a clear pattern to the density estimates: if the inter-trap distance is too small, then the density estimate is too large; and if the inter-trap distance is too large, then the density estimate is too low. This pattern is not a property of the snow leopard simulation as it is also seen when the internal simulation is used to generate the capture matrix. This pattern becomes less pronounced when more effort is applied, but when only 25 cameras are used there are a relatively small number of possible survey designs where unbiased estimates are produced. The guidelines about survey design in the literature as outlined in chapter 2, are not specific enough to guarantee an unbiased density estimate, there are multiple survey design which meet the guidelines but still produce biased estimates of density.

In their paper examining the bias of density estimates from the internal simulation, Tobler and Powell (2013) suggested a minimum of 40-50 cameras per survey, and later went on to call for a survey of at least 100 cameras for jaguars in particular. Whilst it is possible to achieve an unbiased density estimate with 42 cameras, there would be a narrow window of unbiased survey designs. Based on the results

presented here, in order to have confidence in survey designs and results, closer to 100 cameras would be needed. This is suggested because there is a much wider range of unbiased survey designs that could be chosen. The precision of the estimates reduces slowly with effort and peaks when between two and five home ranges are covered. However, even when 100 cameras, were used the coefficient of variation was over 30%. This is higher than is desirable, White (1982), for example, wanted researchers to aim for 10%.

4.4.3 Causes of biased estimates

The internal parameters showed a distinct pattern: g_0 tends to be estimated correctly with small survey areas and inter-trap distances but, as survey area increases, this becomes increasingly poorly estimated. Conversely, the σ values are underestimated when survey area is small. As the survey area increases, the σ tends to the correct value before becoming overestimated. A large g_0 value would result in a lower density estimate, as it implies that a higher proportion of animals are seen than is the reality, and a low σ would result in the effective sampling area being too small and therefore an overestimation of density. This chapter tried to identify what aspects of the capture matrices cause these overestimations and underestimations.

The only guideline currently in the literature for the capture matrix suggests that 20 captures should produce a reliable estimate when using SECR (Gardner et al., 2010b; Sollmann et al., 2012b; Efford et al., 2009). Based on the work presented here, 20 captures is neither a necessary nor a sufficient criterion for an unbiased density estimate (Figure 4.9a, Figure 4.13a). When comparing simulations with the same effort and survey design, more captures resulted in a larger density estimate (Figure 4.9b & Tables C.2 - C.3). However, there was a moderate negative correlation between the number of captures and the estimation of g_0 for large survey areas, as g_0 is generally overestimated at large survey areas. This implies that, as the number of captures increased, g_0 was closer to the true value, showing some utility in greater capture numbers.

The overall impression given from these variables, is that it is important to collect data from a large cross-section of the population with recaptures from many

animals, with the recaptures spread over as large an area as possible. Few studies give the breakdown of captures, however some of those that do show that surveys can be dominated by one individual (Rayan and Mohamad, 2009; Wegge et al., 2004) or one subsection (Gray and Prum, 2012) of the population.

The estimated values of σ are low when the survey area is too small. Few of the variables that were examined correlated with the estimation of σ. The two most significant variables were the average number of cameras an animal visits, and the distances between recaptures. Again, there is cross-correlation between these variables that make regression unadvisable; however, the inference of these results is that capture of as many animals as possible captured across their home range is important for the estimation of σ and, therefore, density.

The results in this section show that the placement of captures are important in this methodology: this is something that, to the best of my knowledge, has not been acknowledged in the literature before now. Collecting more than 20 captures does not guarantee an unbiased result and, all other things being equal, more captures will result in a higher estimate, not a better estimate. Out of the four guidelines that were examined in this chapter, a study achieving more than 20 captures performed the worst, whilst a guideline of capturing over 20% of the animals and covering at least 50% of the home range performed the best. Therefore, in order to create a study with good g_0 and σ estimates, and so an unbiased density estimate, it is important to collect a sample that has sampled animals evenly, and across their home ranges.

Unfortunately, whilst the guideline of at least 20% of the animals and at least 50% of the home range works very well here, it is impossible for a researcher to implement precisely as they do not know the true population and they may not have a reliable estimate of the average home range. Nevertheless, this result is still useful to researchers because it a) provides a target and b) allows researchers who can form an educated guess for animal numbers and home range to evaluate their study. For example, if these guidelines were used to examine the results from (Alexander et al., 2015), then the conclusion could be that the results were not systematically

biased. Alexander et al. (2015) caught 20 individuals, and using CMR to estimate abundance resulted in an approximate abundance of 27 animals (95% CI: 20 - 36 animals). Even if the highest estimate of abundance was correct, Alexander et al. (2015) would have caught more than 20% of the population. In addition Alexander et al. (2015) reported a mean maximum distance moved (MMDM) of 7.60 km. If this was the maximum distance between recaptures then, as long as the average home range was less than 180 km^2, the estimate would be unbiased. However, because the MMDM is a mean, it is less than the maximum distance between recaptures for a single animal. Therefore, as long as the maximum distance is 11 km it would be unbiased for an average home range of 360 km^2, the average home range used in simulation in this chapter.

4.4.4 Comparison with internal simulations

Other researchers have suggested that it is good practice to use the internal simulation to check their survey designs (Tobler and Powell, 2013). Whilst, in theory, using a tool to check survey design is a very important step, the results in this chapter show that there may be a difference between the estimated bias in the internal simulation and the bias in the real world. If the simulation of movement is an accurate representation of snow leopard movement, then the internal simulation would have suggested that survey designs that produced biased estimates of density were unbiased.

The results of this study suggest that the SECR density estimation is more sensitive to changes in survey area then originally assumed based on internal simulation. Using the snow leopard movement model, the SECR produces larger biases as a result of survey density which deviates from an optimal configuration. This implies that the movement of the animal is an important factor in the reliability of the density estimate. Because realistic movement has never been studied before as in this thesis, it has not been suggested that that SECR is more sensitive to change is survey area than previously thought. However, because the internal simulation is less sensitive, the results could produce false confidence in survey designs, and therefore additional care should be taken.

4.5 Conclusions

As the movement model used in this simulation is based on one species in one location, the results that were found may only be applicable in these circumstances. However, I conclude that SECR is sensitive to changes in movement patterns, so using the internal SECR model in R to test layouts may not work as well as previously hoped. This chapter also concludes that the distribution of captures over animals and space is important, and that looking at the number of captures is neither a necessary or sufficient condition for a unbiased estimate. This could be good news for researchers who study animals with low recapture rates, like Weingarth et al. (2015) who struggled to reach 20 captures with violating closure. Based on the results of this chapter, they can obtain unbiased estimates with fewer captures, if they can achieve captures of a larger proportion of the population.

SECR can estimate density of the target species well, even when the movement patterns of the animal do not match the assumptions of the model. However, it is important that sufficient effort is used. Like previous studies, the results here show that the current field surveys are using too few cameras to estimate density reliably, giving them a relatively small range of unbiased survey designs from which to choose. In addition, based on the results in this chapter, a survey area less than one home range and with fewer than five cameras per home range would result in biased estimates. Whilst the layout requirements are a good start for designing a survey, they would be the minimum requirements as the layout guidelines are not a guarantee of an unbiased result. This chapter also demonstrates that researchers should collect as large a proportion of animals as possible, and have at least one animal captured widely across their home range. By doing this, researchers are reducing the bias in the internal g_0 and σ estimates, and so in turn, the density estimate. Combining camera trap surveys with additional telemetry studies might improve knowledge of home ranges, such that better population coverage may be achieved.

4.5.1 Further work

A sensitivity analysis to examine the parameter space of the current model would not only show how sensitive the current model is to changes in parameters such as speed, turn angle distribution, home range size, and survey duration. It might show applicable the model is for other species. If the conclusions remained constant regardless of changes in a parameter then it would also show how the conclusions are relevant to many more species.

There are many possible expansions of this model to make it a more realistic simulation, and more applicable to other species. For example, in many field surveys, the capture rates for males and females are not equal (Sollmann et al., 2011). A further step here could be to investigate the effect this has on results by changing the capture rate for males and females. In this simulation, that would be done artificially by altering the radius of the camera in the simulation. Another possible change would be to simulate for species that have non-overlapping home ranges between animals of the same sex. This would make the results more applicable to other species of felid such as tigers. Running the simulation based on other movement models would add to the impact of this work, as it would be possible to tell whether the guidelines produced here are species-specific or could cover a wider range of animals. Finally, adding topography would be interesting, to coincide with the work of least cost paths that Royle et al. (2013a) has published.

Ideally, the new guidelines would be tested in a known environment in order to assess them in the field. However, such an environment is hard to find and the experiments would be costly. Consequently, creating a simulation based on a dataset from a different species would allow the guidelines to be examined on the basis of on different ecological characteristics.

Chapter 5

It's the end of the world as we know it: a generalised REM method of estimating animal density

Contents

5.1 Introduction

Animal population density is one of the fundamental measures in ecology and conservation. It has important implications for a range of issues such as sensitivity to stochastic fluctuations (Richter-Dyn and Goel, 1972; Wright and Hubbell, 1983) and risk of extinction (Purvis et al., 2000). Monitoring animal population changes in response to anthropogenic pressure is becoming increasingly important as humans rapidly modify habitats and change climates (Everatt et al., 2014). Sensor technology, such as camera traps (Karanth, 1995; Rowcliffe and Carbone, 2008) and acoustic detectors (Clark, 1995; Acevedo and Villanueva-Rivera, 2006; Walters et al., 2012) are becoming widely used to monitor changes in animal populations (Rowcliffe and Carbone, 2008; Kessel et al., 2014; Walters et al., 2013). As the new technology is efficient, relativity cheap and non-invasive (Cutler and Swann, 1999), it allows for surveys to be conducted over large areas and for long periods. However, converting sampled count data into estimates of density is problematic as the detectability of animals needs to be accounted for (Anderson, 2001).

5.1.1 Generalisation of the random encounter model

Existing methods for estimating animal density often require information that is unavailable. For example, capture-mark-recapture methods (Karanth, 1995; Trolle et al., 2007; Borchers et al., 2014) require recognition of individuals, and distance methods (Harris et al., 2013) require estimates of how far away individuals are from the sensor (Barlow and Taylor, 2005; Marques et al., 2011a). When individuals cannot be told apart, an extension of occupancy modelling can be used to

estimate absolute abundance (Royle and Nichols, 2003). However, as the model is originally formulated to estimate occupancy, count information is simplified to presence-absence data. Assumptions about the distribution of individuals within a space (e.g. a Poisson distribution) must also be made (Royle and Nichols, 2003), and this may be a poor assumption for non-randomly distributed species. Independent surveys must be performed and the definition of a "site" can be difficult, especially for wide-ranging species (MacKenzie and Royle, 2005).

More recently, the development of the random encounter model (REM), a modification of an ideal gas model (Yapp, 1956; Hutchinson and Waser, 2007), has enabled animal densities to be estimated from unmarked individuals of a known speed, and with known sensor detection parameters (Rowcliffe et al., 2008). The REM method has been successfully applied to estimate animal densities from camera trap surveys (Manzo et al., 2012; Zero et al., 2013). However, extending the REM method to other types of sensors (e.g., acoustic detectors) is more problematic, because the original derivation assumes a relatively narrow sensor width (up to $\pi/2$ radians) and that the animal is equally detectable irrespective of its heading (Rowcliffe et al., 2008).

Whilst these restrictions are not problematic for most camera trap makes (e.g., Reconyx, Cuddeback), the REM cannot be used to estimate densities from camera traps with a wider sensor width (e.g. canopy monitoring with fish eye lenses, (Brusa and Bunker, 2014)). Additionally, the REM method is not useful in estimating densities from acoustic survey data as acoustic detector angles are often wider than $\pi/2$ radians. Acoustic detectors are designed for a range of diverse tasks and environments (Kessel et al., 2014), which naturally leads to a wide range of sensor detection widths and detection distances. In addition to this, calls emitted by many animals are directional (Blumstein et al., 2011), breaking the assumption of the REM method.

There has been a sharp rise in interest around passive acoustic detectors in recent years, with a 10 fold increase in publications in the decade between 2000 and 2010 (Kessel et al., 2014). Acoustic monitoring is being developed to study many

aspects of ecology, including the interactions of animals and their environments (Blumstein et al., 2011; Rogers et al., 2013), the presence and relative abundances of species (Marcoux et al., 2011), biodiversity of an area (Depraetere et al., 2012), and monitoring population trends (Walters et al., 2013).

Acoustic data suffers from many of the problems associated with data from camera trap surveys in that individuals are often unmarked, making capture-mark-recapture methods more difficult to use (Marques et al., 2013). In some cases, the distance between the animal and the sensor is known, for example when an array of sensors is deployed and the position of the animal is estimated by triangulation (Lewis et al., 2007b). In these situations distance-sampling methods can be applied, a method typically used for marine mammals (Rogers et al., 2013). However, in many cases distance estimation is not possible, for example when single sensors are deployed, a situation typical in the majority of terrestrial acoustic surveys (Elphick, 2008; Buckland et al., 2008). In these cases, only relative measures of local abundance can be calculated, and not absolute densities. This means that comparison of populations between species and sites is problematic without assuming equal detectability (Hayes, 2000; Schmidt, 2003; Walters et al., 2013). Equal detectability is unlikely because of differences in environmental conditions, sensor type, habitat, and species biology.

5.1.2 Generalised random encounter model for cryptic species

Rowcliffe et al. (2008) published the random encounter model (REM) to estimate the density of animals based on count data collected from camera surveys, and was based on the principles of particle interaction laid out in Yapp's gas model (Yapp, 1956). The REM is derived assuming a stationary sensor with a detection width less than $\pi/2$ radians. However, in order to apply this approach more generally, and in particular to stationary acoustic detectors, the constraint on the sensor detection width needs to be relaxed, and the technique extended to allow for animals with directional signals. This adaption of the REM was made by Lucas et al. (2015) to form the generalised random encounter model (gREM) in 2015 (Lucas et al., 2015). The gREM allows detection width, θ, between 0 and 2π with a detection distance r

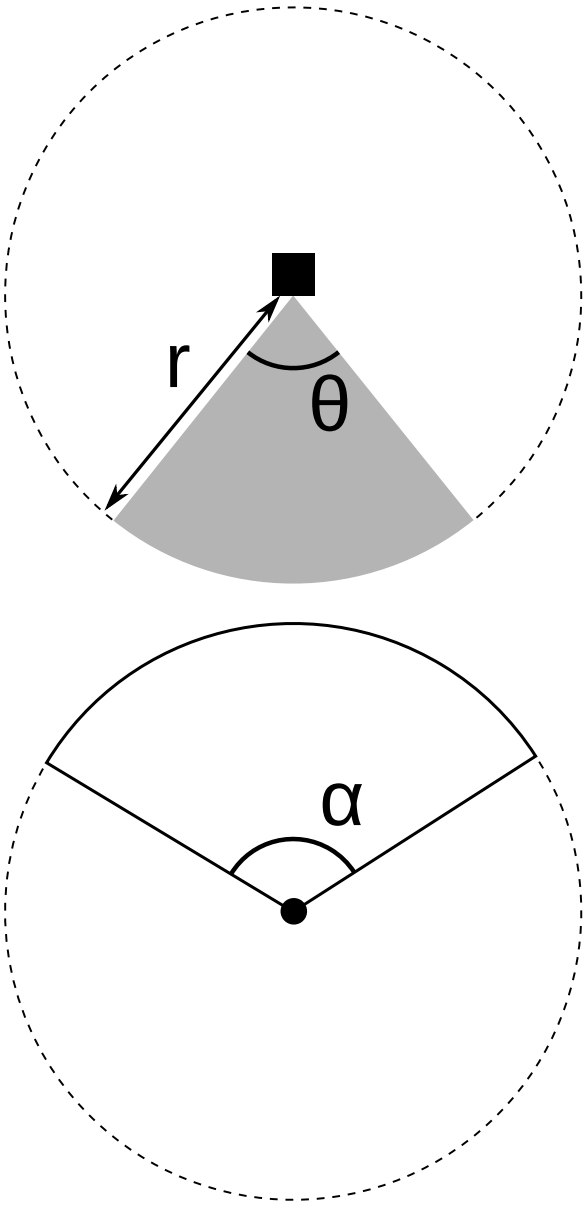


Figure 5.1: Representation of sensor detection width and animal signal width. The filled square and circle represent a sensor and an animal, respectively; θ, sensor detection width (radians); r, sensor detection distance; dark grey shaded area, sensor detection zone; α, animal signal width (radians). Dashed lines around the filled square and circle represents the maximum extent of θ and α, respectively.

giving a circular sector within which animals can be captured (the detection zone) (Figure 5.1). Additionally, animals were modelled as having an associated signal width α between 0 and 2π (Figure 5.1, see Appendix D for a list of symbols). The interaction between the signal and the sensor is characterised by the profile width, $\bar{p}$, and this is fed into the the gas model equation in order to estimate density (Equation 5.1).

$$D = z/vt\bar{p}. \tag{5.1}$$

Where D is Density, z is the number of captures, t is the length of the survey and $\bar{p}$ is the profile width. $\bar{p}$ is the average width of the detection zone with a fixed detection angle and signal angle, over all possible directions of movement through the detection zone.

Rather than having one equation that describes $\bar{p}$ globally, the gREM must be split into submodels due to discontinuous changes in p as α and θ change (the angle of signal emitted by an animal, and the angle of the detector). These discontinuities can occur for a number of reasons such as a profile switching between being limited by α and θ, the difference between very small profiles and profiles of size zero, and the fact that the width of a sector stops increasing once the central angle reaches π radians (i.e., a semi-circle is just as wide as a full circle). For different combinations of α and θ, different models were needed, resulting in the creation of eight gREM submodels. A full derivation of the gREM can be found in Lucas et al. (2015).

Any estimate of density would require prior knowledge of animal velocity and call width v and α taken from other sources e.g. the literature (Brinkløv et al., 2011; Carbone et al., 2005) and sensor width and radius, θ and r which can be measured or obtained from manufacturer specifications (Holderied and Von Helversen, 2003; Adams et al., 2012). However, there are a number of assumptions in the model that in reality do not hold. For example, signal emission is rarely cone shaped, the volume and intensity of the call is not uniform variation across the signal.

5.1.3 Aims for the chapter

Chapter 2 and chapter 4 showed that CMR and SECR models produce biased results when a typical level of effort is used on low density species such as snow leopards and other felids. This chapter examines whether another method of studying felids might be possible. Therefore it uses the simulation created in chapter 3 to establish the suitability of REM as an appropriate method for monitoring snow leopard density. This shows that REM is still an appropriate method when a complex movement pattern is used, but also allows us to calculate how many cameras would be needed to have a good estimate of low density animals such as snow leopards.

This chapter also examines the generalisation of the REM (gREM) as an extension to the camera trap model of Rowcliffe et al. (2008). The gREM estimates absolute density from count data from acoustic detectors, or camera traps, where the sensor width can vary from 0 to 2π radians, and the signal given from the animal can be directional. The accuracy and precision of the gREM are assessed within a simulated environment, by varying the sensor detection widths, animal signal widths, number of captures and models of animal movement. The simulation results are used to recommend best survey practice for estimating animal densities from remote sensors, both acoustic recorders or camera traps.

5.2 Methods

5.2.1 Simulation testing of the gREM for acoustic monitoring

In order to test the gREM, additional simulations were created. In the field, the gREM may be used on animals with much higher densities than snow leopards, and with different movement patterns. Therefore, as a test of principle, the gREM was first tested with a number high density of animals within the simulation, and simpler movement models.

The accuracy and precision of the gREM was tested by developing a spatially explicit simulation of the interaction of sensors and animals using different combinations of sensor detection widths, animal signal widths, number of captures, and models of animal movement. One hundred simulations were run where each con-

sisted of a 7.5 km by 7.5 km square with periodic boundaries. A periodic boundary is when an animal leaves the simulation on one side it reappears on the other, effectively making the world a torus shape. A stationary sensor of radius $r = 10$ m, was set up in the exact centre of each simulated study area, covering seven sensor detection widths θ, between 0 and 2π ($2/9\pi$, $4/9\pi$, $6/9\pi$, $8/9\pi$, $10/9\pi$, $14/9\pi$, and 2π). Each sensor was set to record continuously and to capture animal signals effectively instantaneously from emission. Each simulation was populated with a density of 70 animals km^{-2}, calculated from the equation in Damuth (1981) as the expected density of mammals weighing 1 g. This density therefore represents a reasonable estimate of density of individuals, given that the smallest mammal is around 2 g (Jones et al., 2009). A total of 3937 individuals per simulation was created which were placed randomly at the start of the simulation. 11 signal widths α between 0 and π were used ($1/11\pi$, $2/11\pi$, $3/11\pi$, $4/11\pi$, $5/11\pi$, $6/11\pi$, $7/11\pi$, $8/11\pi$, $9/11\pi$, $10/11\pi$, π).

Each simulation lasted for N steps (14400) of duration T (15 minutes), giving a total duration of 150 days. The individuals moved within each step with a distance d, with an average speed, v. The distance, d, was sampled from a normal distribution with mean distance, $\mu_d = vT$, and standard deviation, $\sigma_d = vT/10$, where the standard deviation was chosen to scale with the average distance travelled. The choice of $\sigma_d = vT/10$ as standard deviation was arbitrary, other values were used in experimentation and showed no substantial variations. An average speed, $v = 40$ km day^{-1}, was chosen based on the largest day range of terrestrial animals (Carbone et al., 2005), and represents the upper limit of realistic speeds. At the end of each step, individuals were allowed to either remain stationary for a time step (with a given probability, S), or change direction where the change in direction has a uniform distribution in the interval $[-A, A]$. This resulted in seven different movement models: (1) simple movement, where S and $A = 0$; (2) stop-start movement, where (i) $S = 0.25$, $A = 0$, (ii) $S = 0.5$, $A = 0$, (iii) $S = 0.75$, $A = 0$; (3) correlated random walk movement, where (i) $S = 0$, $A = \pi/3$, (ii) $S = 0$, $A = 2\pi/3$, iii) $S = 0$, $A = \pi$.

Individuals were counted as they moved into the detection zone of the sensor per simulation.

The estimated animal density was calculated from the gREM by summing the number of captures per simulation and inputting these values into the correct gREM submodel. The accuracy of the gREM was determined by comparing the true simulation density with the estimated density. Precision of the gREM was determined by the standard deviation of estimated densities. This method was used to compare the accuracy and precision of all the gREM submodels. As these submodels are derived for different combinations of α and θ, the accuracy and precision of the submodels was used to determine the impact of different values of α and θ.

The influence of the number of captures and animal movement models on accuracy and precision was investigated using four different gREM submodels representative of the range of α and θ values (submodels NW1, SW1, NE1, and SE3, Figure D.1). From a random starting point, the simulation was run until a range of different capture numbers were recorded (from 10 to 100 captures), recorded the length of time this took, and estimated the animal density for each of the four sub-models. These estimated densities were compared to the true density to assess the impact on the accuracy and precision of the gREM. The coefficient of variation was calculated in order to compare the precision of the density estimates from simulations with different expected numbers of captures. The gREM also assumes that individuals move continuously with straight-line movement (simple movement model) and therefore an assessment on the impact of breaking the gREM assumptions was made. Four submodels were used to compare the accuracy and precision of a simple movement model, stop-start movement models (using different average amounts of time spent stationary), and random walk movement models. As the parameters (α, β, r and v) are likely to be measured with error, a sensitivity analysis of the impact of measurement errors was completed. In the sensitivity analysis errors, of 0%, $\pm$5% and $\pm$10% were used.

5.2.2 Testing of the REM as a method for monitoring felids

Finally, the accuracy and precision of the gREM was considered for the case of snow leopards, by using the movement model created in chapter 3 and chapter 4, and setting the r, θ and α to 10 m, 2π and $\pi/6$ respectively. The density of animals in the simulation was set to 0.008 animals km^{-2}, as discussed in chapter 4, and the average speed to approximately 5.27 $\mathrm{km\,day}^{-1}$. Two situations were considered, a survey with 26 cameras and a survey with 43 cameras, as these represented the median and mean number of cameras available for researchers (Appendix A.2). The simulation was run for six years, and the density estimated every two months, to find the optimal length for a gREM study on snow leopards. Based on the current understanding of the REM; the REM should not be sensitive to seasonal effects of behaviour. However, there would be fluctuations in animal density that might make the REM unreliable. Whilst six years would be too long to run a study in practice, running the simulation like this was intended to show the scope of the problem.

5.3 Results

5.3.1 gREM submodel accuracy and precision

All gREM submodels showed a high accuracy, i.e., the mean difference between the estimated and actual values was not significantly different from zero across all models (Figure 5.2). However, the precision of the submodels does vary, where the gas model is the most precise and the SW7 sub model the least precise, having the smallest and the largest interquartile range, respectively (Figure 5.2). The standard deviation of the error between the estimated and true densities is strongly related to both the sensor and signal widths (Appendix S5), such that larger widths have lower standard deviations (greater precision) due to the increased capture rate of these models.

5.3.2 Effect of number of captures on accuracy of model

Within the four gREM submodels tested (NW1, SW1, SE3, NE1), the accuracy was not affected by the number of captures. The mean difference between the estimated and actual values was not significantly different from zero across all capture rates

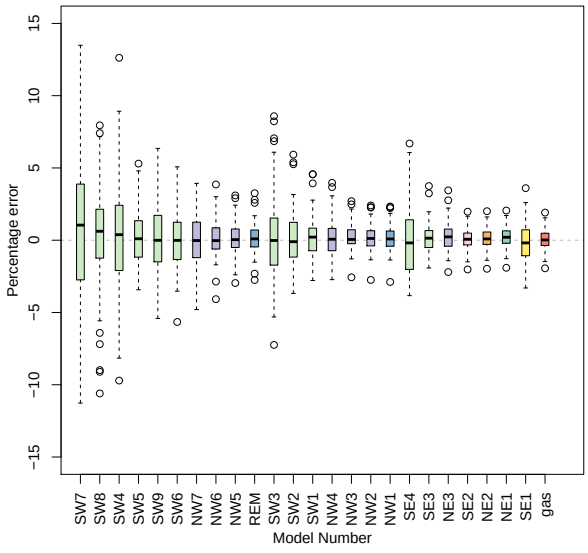


Figure 5.2: Simulation model results of the accuracy and precision for gREM submodels. The percentage error between estimated and true density for each gREM sub model is shown within each box plot, where the black line represents the median percentage error across all simulations, boxes represent the middle 50% of the data, whiskers represent variability outside the upper and lower quartiles with outliers plotted as individual points. Box colours correspond to the expressions for average profile width $\bar{p}$ given in Figure 4.

(Figure 5.3). However, the precision was dependent on the number of captures across all four of the gREM submodels, where precision increases as number of captures increases, as would be expected for any statistical estimate (Figure 5.3). For all gREM submodels, the coefficient of variation falls to 10% at 100 captures.

5.3.3 Effect of movement models

Within the four gREM submodels tested (NW1, SW1, SE3, NE1), neither the accuracy or precision was affected by the average amount of time spent stationary: the mean difference between the estimated and actual values was not significantly different from zero for each category of stationary time (0, 0.25, 0.5 and 0.75) (Figure 5.4). Altering the maximum change in direction in each step (0, $\pi/3$, $2\pi/3$, and π) did not affect the accuracy or precision of the four gREM submodels (Figure 5.5).

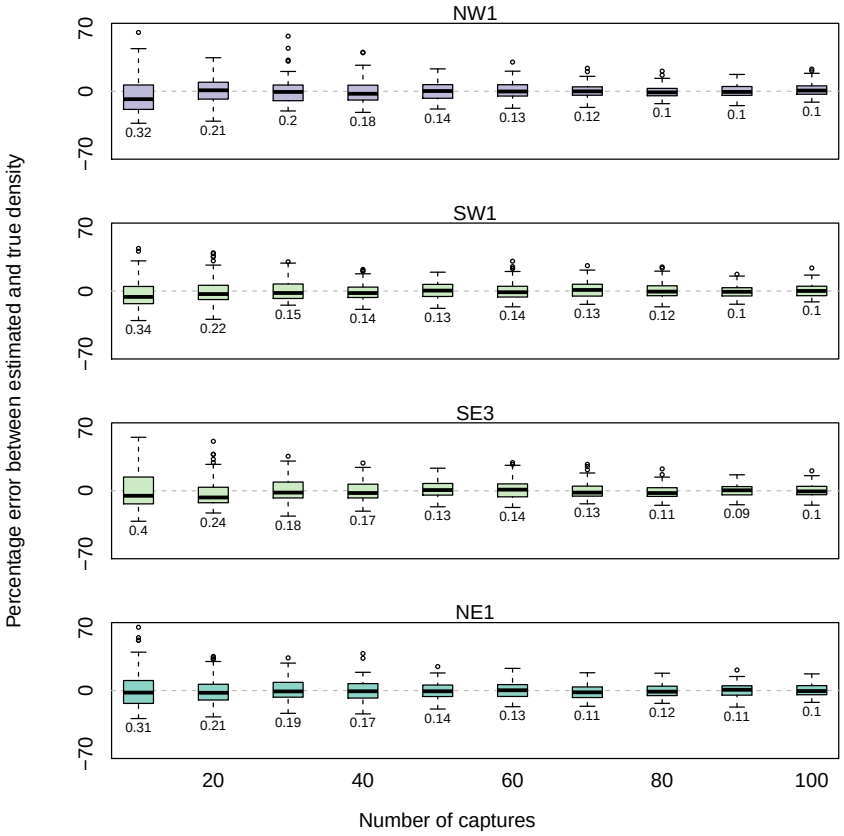


Figure 5.3: Simulation model results of the accuracy and precision of four gREM submodels (NW1, SW1, SE3 and NE1) given different numbers of captures. The percentage error between estimated and true density within each gREM sub model for capture rate is shown within each box plot, where the black line represents the median percentage error across all simulations, boxes represent the middle 50% of the data, whiskers represent variability outside the upper and lower quartiles with outliers plotted as individual points. Sensor and signal widths vary between submodels. The numbers beneath each plot represent the coefficient of variation. The colour of each box plot corresponds to the expressions for average profile width $\bar{p}$ given in Figure D.1

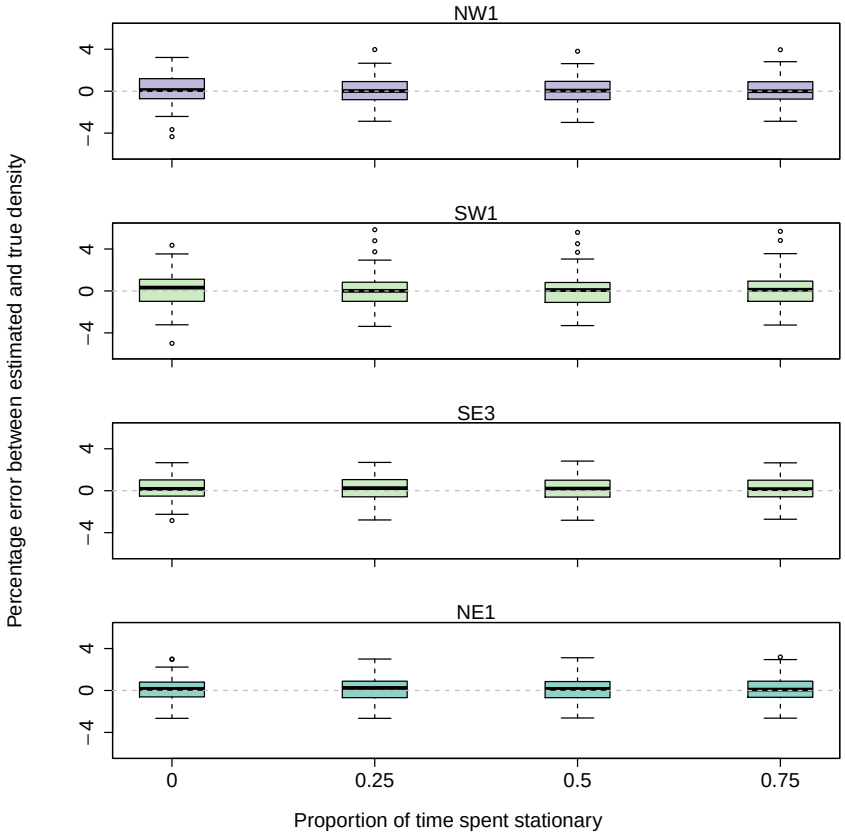


Figure 5.4: Simulation model results of the accuracy and precision of four gREM submodels (NW1, SW1, SE3 and NE1) given different movement models where the average amount of time spent stationary (stop-start movement) varies. The percentage error between estimated and true density within each gREM sub model for the different movement models is shown within each box plot, where the black line represents the median percentage error across all simulations, boxes represent the middle 50% of the data, whiskers represent variability outside the upper and lower quartiles with outliers plotted as individual points. The simple model is represented where time and maximum change in direction equals 0. The colour of each box plot corresponds to the expressions for average profile width $\bar{p}$ given in Figure D.1

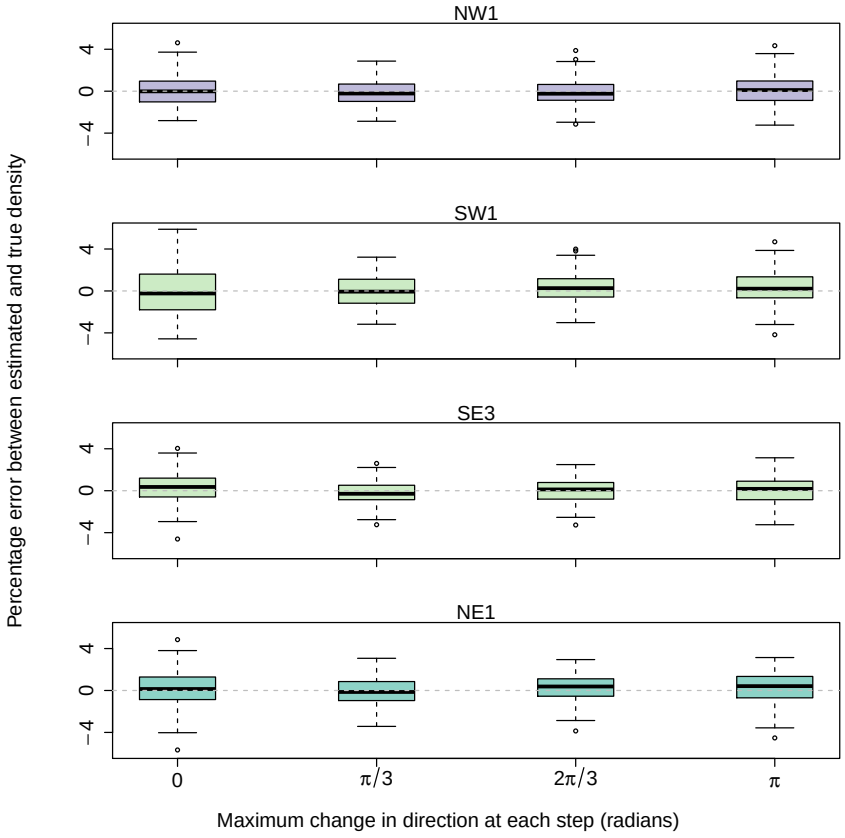


Figure 5.5: Simulation model results of the accuracy and precision of four gREM submodels (NW1, SW1, SE3 and NE1) given different movement models where the maximum change in direction at each step (correlated random walk model) varies. The percentage error between estimated and true density within each gREM sub model for the different movement models is shown within each box plot, where the black line represents the median percentage error across all simulations, boxes represent the middle 50% of the data, whiskers represent variability outside the upper and lower quartiles with outliers plotted as individual points. The simple model is represented where time and maximum change in direction equals 0. The colour of each box plot corresponds to the expressions for average profile width $\bar{p}$ given in Figure D.1

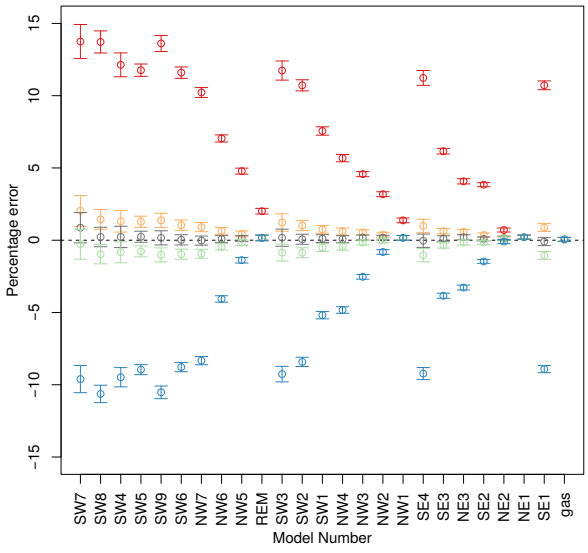


Figure 5.6: Percentage error of the density estimate when incorrect signal width is used. For each point on the graph the circle represents mean error and the bars either side represent the 95% confidence interval. Red, yellow, green and blue represent a 10%, 5%, 0% underestimation and 5% and 10% overestimation of signal width respectively.

5.3.4 Impact of parameter error

The percentage error in the density estimates across all parameters and gREM submodels shows a similar response for under- and over-estimated parameters, suggesting the accuracy is reasonable with respect to parameter error (Figure 5.6 - 5.9). The impact of parameter error on the precision of the density estimate varies across and gREM submodels and parameters, where α shows the largest variation including the largest values. However, in all cases, the density estimate percentage error is not more than 5% greater than the error in the parameter estimate (Figure 5.6 - 5.9).

5.3.5 Suitability of density estimation using the gREM for snow leopards

The low density of the snow leopard population, and the median and mean number of cameras being 26 and 43, respectively, results in few captures being recorded. The average number of captures for 26 and 43 cameras over the two month survey

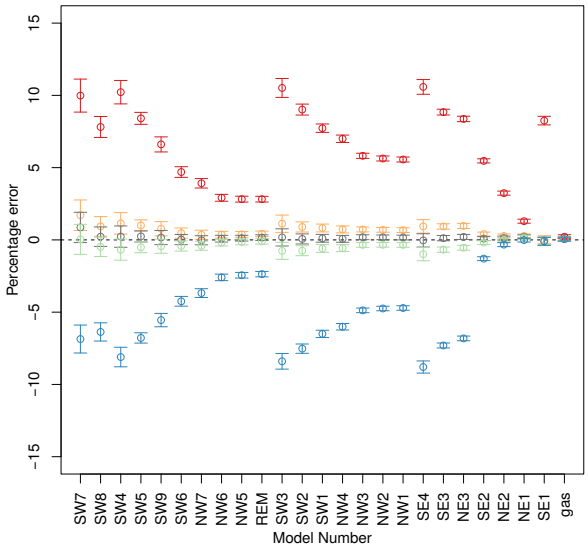


Figure 5.7: Percentage error of the density estimate when incorrect detection width is used. For each point on the graph the circle represents mean error and the bars either side represent the 95% confidence interval. Red, yellow, green and blue represent a 10%, 5%, 0% underestimation and 5% and 10% overestimation of detection width respectively.

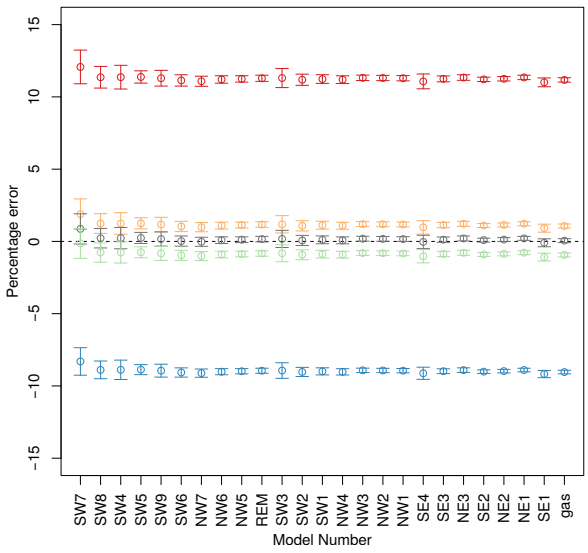


Figure 5.8: Percentage error of the density estimate when incorrect radius is used. For each point on the graph the circle represents mean error and the bars either side represent the 95% confidence interval. Red, yellow, green and blue represent a 10%, 5%, 0% underestimation and 5% and 10% overestimation of the length of the radius respectively.

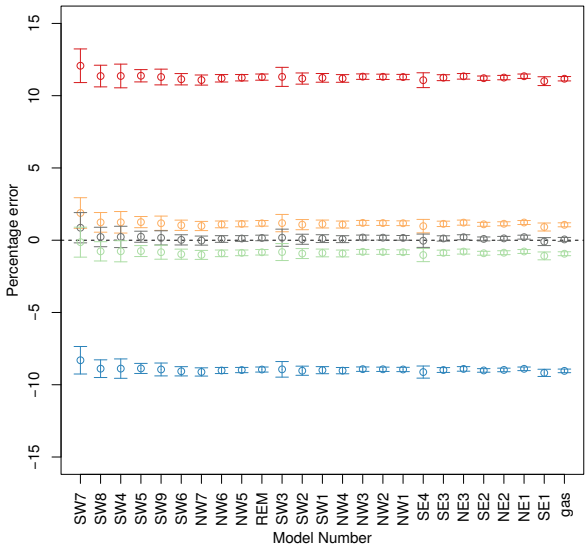


Figure 5.9: Percentage error of the density estimate when incorrect speed estimate is used. For each point on the graph the circle represents mean error and the bars either side represent the 95% confidence interval. Red, yellow, green and blue represent a 10%, 5%, 0% underestimation and 5% and 10% overestimation of the estimated average speed respectively.

period is 0.6 and 1 respectively (Figure 5.10 - 5.11). The Wilcoxon test was used to test the median value estimated by the gREM and the true density and, when corrected for multiple testing, this showed no significant difference between the estimated and true value for 26 or 43 cameras. Whilst the gREM is accurate under these conditions, it is not precise: the coefficient of variation for 26 and 43 cameras was 103% and 138% respectively. Even after six years of survey effort, the coefficient of variation for 26 and 43 cameras was 22% and 18% respectively

5.4 Discussion

5.4.1 Analytical model

The gREM was developed to estimate density from acoustic sensors and camera traps. This has entailed a generalisation of the gas model and the REM in Rowcliffe et al. (2008) to be applicable to any combination of sensor width θ and signal directionality α. It is emphasised here that the approach is robust to multiple detections of the same individual within a survey and does not require cases of multiple

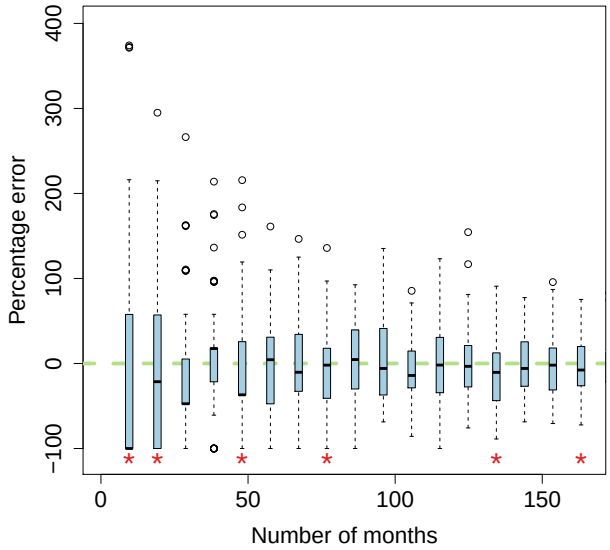


Figure 5.10: Each box plot shows the percentage error for a given number of months effort for 26 cameras, when the original REM model is applied to a simulation of snow leopard movement. The percentage error between estimated and true density within each gREM sub model for capture rate is shown within each box plot, where the black line represents the median percentage error across all simulations, boxes represent the middle 50% of the data, whiskers represent variability outside the upper and lower quartiles with outliers plotted as individual points. Red represent a significant difference between the estimated median density being and the true density at the 0.05 level, when multiple testing is not accounted for.

capture to be removed or recorded. Simulations have been used to show, as a proof of principle, that these models are accurate and precise under the conditions tested. The precision of the gREM was found to be dependent on the number of captures which, in turn, depends on the width of the sensor and the signal.

There are a number of possible extensions to the gREM that could be developed in the future. The original gas model was formulated for the case where both subjects, either animal and sensor, or animal and animal, are moving (Hutchinson and Waser, 2007). Indeed, any of the models with animals that are equally detectable in all directions ($\alpha = 2\pi$) can be trivially expanded by replacing animal speed v with $v + v_s$ where v_s is the speed of the sensor. However, when the animal has a directional call, as seen in both terrestrial and aquatic environments (Lammers and Au, 2003; Blumstein et al., 2011), the extension becomes less simple. The ap-

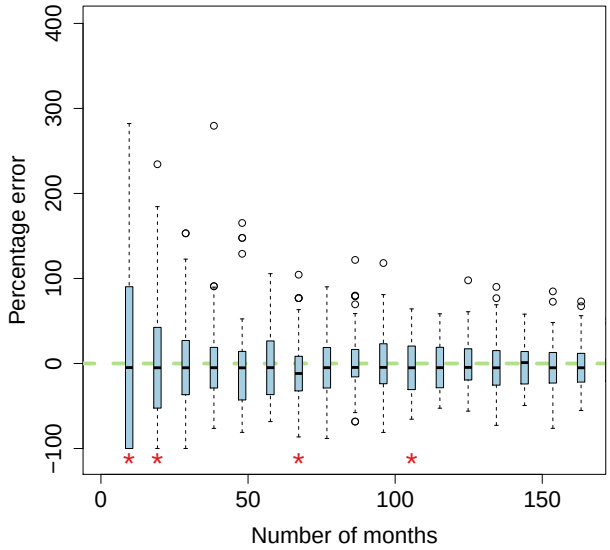


Figure 5.11: Each box plot shows the percentage error for a given number of months effort for 43 cameras, when the original REM model is applied to a simulation of snow leopard movement. The percentage error between estimated and true density within each gREM sub model for capture rate is shown within each box plot, where the black line represents the median percentage error across all simulations, boxes represent the middle 50% of the data, whiskers represent variability outside the upper and lower quartiles with outliers plotted as individual points. Red represent a significant difference between the estimated median density being and the true density at the 0.05 level, when multiple testing is not accounted for.

proach would be to calculate again the mean profile width. However, for each angle of approach, one would have to average the profile width for an animal facing in any direction (i.e., not necessarily moving towards the sensor) weighted by the relative velocity of that direction. There are a number of situations where a moving detector and animal could occur, e.g. an acoustic detector towed from a boat when studying porpoises (Kimura et al., 2014) or surveying echolocating bats from a moving car (Ahlen and Baagøe, 1999; Jones et al., 2013).

Interesting but unstudied problems impacting the gREM are, firstly, edge effects caused by sensor trigger delays (the delay between sensing an animal and attempting to record the encounter) (Rovero et al., 2013), and, secondly, sensors that repeatedly turn on an off during sampling (Jones et al., 2013). The second problem is particularly relevant to acoustic detectors that record ultrasound by time

expansion. Here, ultrasound is recorded for a set time period and then slowed down and played back, rendering the sensor 'deaf' periodically during sampling. Both of these problems may cause biases in the gREM, as animals can move through the detection zone without being detected. As the gREM assumes constant surveillance, the error created by switching the sensor on and off quickly will become more important if the sensor is only on for short periods of time. For example, if it takes longer for the recording device to be switched on than the length of some animal calls, then there could be a systematic underestimation of density. We recommend that the gREM is applied to constantly sampled data, and the impacts of breaking these assumptions on the gREM should be further explored.

5.4.2 Accuracy, Precision and Recommendations for Best Practice

Based on our simulations, we believe that the gREM has the potential to produce accurate estimates for many different species, using either camera traps or acoustic detectors. However, the precision of the gREM differed between submodels. For example, when the sensor and signal width were small, the precision of the model was reduced. Therefore, when choosing a sensor for use in a gREM study, the sensor detection width should be maximised. If the study species has a narrow signal directionality, other aspects of the study protocol, such as length of the survey, should be used to compensate.

The precision of the gREM is greatly affected by the number of captures. The coefficient of variation falls dramatically between 10 and 60 captures and then, after this, continues to reduce slowly. At 100 captures the submodels reach 10% coefficient of variation, considered to a very good level of precision (Thomas and Marques, 2012; White, 1982). Many current studies do not reach this level of precision, (O'Brien et al., 2003; Proctor et al., 2010; Foster and Harmsen, 2012). The length of surveys in the field will need to be adjusted so that enough data can be collected to reach this precision level. Populations of fast moving animals or populations with high densities will require less survey effort than those species that are slow moving or have populations with low densities. In addition, if a species is

evenly distributed over an area than a smaller survey area becomes representative, and therefore less effort would be required.

The gREM was both accurate and precise for all the movement models we tested (stop-start movement and correlated random walks). The precision of the gREM may be affected by the interaction between the movement model and the size of the detection radius. We have studied a relatively long step length compared to the size of the detection radius, and therefore the chance of catching the same animal multiple times within a short space of time was reduced. As a results there is little effect on the precision of the model (Figure 5.5). However, if the ratio of step length to detection radius was smaller, then the precision of the model may be decreased (but with no effect on its accuracy).

It was found that the sensitivity of the gREM to inaccurate input parameter estimates was both predictable and reasonable, although this varies between different parameters and gREM submodels. Care should be taken while estimating these parameters when analysing both acoustic and camera trap data; however, acoustic data poses particular problems. (Rowcliffe et al., 2011) researched estimates for r (detection distance) and θ (sensor width) for REM studies. (Rowcliffe et al., 2011) found that these parameters are dependent on the size of the species being studied, and the time and location of the study, therefore it is important for a researcher to examine these before calculating density. When estimating animal movement speed v, only the speed of movement during the survey period should be used. Based on the simple simulation in this chapter the signal width is the most sensitive parameter to inaccurate estimates. However there are many factors that are not taken into account, and more in depth studies would be required to confirm this. In the case of snow leopards, and other species that use camera traps, the signal with is simply 2π, as the animal is identifiable from all angles and there should be no error from this variable.

Running the simulation to replicate snow leopard movement shows that, for low density animals, where low capture rates could be expected, the REM may not be a suitable method of estimating density. Whilst the method was accurate for 26

and 43 cameras, the method was not precise. More than six years worth of survey effort would be required in order to reduce the coefficient of variation to below 10%, and collect over 100 captures. In order for this method to be used in the field over a period of two to three months, a researcher would require more than 1000 cameras, and therefore it is unlikely that this method would represent a sensible method of density estimation for this species.

5.4.3 Limitations

Although we have used simulations to validate the gREM submodels, much more robust testing is needed. Although difficult, proper field test validation would be required before the models could be fully trusted. The REM (Rowcliffe et al., 2008) has already been field tested, and both Rowcliffe et al. (2008) and Zero et al. (2013) both found that the REM was an effective manner of estimating animal densities (Rowcliffe et al., 2008; Zero et al., 2013). In some taxa, gold standard methods of estimating animal density exist, such as capture-mark-recapture (Sollmann et al., 2013a). Where these gold standards exist or true numbers are known, a simultaneous gREM study could be completed to test the accuracy under field conditions, similar to the tests in (Rowcliffe et al., 2008). An easier way to continue to evaluate the models is to run more extensive simulations which break the assumptions of the analytical models.

Within the simulation it was assumed there was an equal density across the study area; however, in a field environment, the situation would be much more complex, with additional variation coming from local changes in density between sensor sites. Though, theoretically, unequal densities should not affect accuracy (Hutchinson and Waser, 2007), this will affect precision and further simulations should be used to quantify this effect. We allowed the sensor to be stationary and continuously detecting, negating the triggering, and non-continuous recording issues that could exist with some sensors. In the simulation, animals moved at a speed of $40\,\mathrm{km\,day^{-1}}$, equivalent to the largest day range of terrestrial animals (Carbone et al., 2005). Other speed values should not alter the accuracy of the gREM; however, precision would be affected, all else being equal, since slower speeds produce

fewer records. We also assume perfect knowledge of the average speed of an animal and size of the detection zone. All of which may lead to possible bias or a decrease in precision.

Detection probability is a major focus for methods estimating density. The gREM does not fit a statistical model to estimate detection probability as occupancy models and distance sampling do (Royle and Nichols, 2003; Barlow and Taylor, 2005; Marques et al., 2011a). Instead, it explicitly models the process, with animals only being detected if they approach the sensor from a suitable direction. More detailed models of this process could include the regularity of acoustic calls or other details. It is also assumed that the detection is perfect inside the detection zone, and non-existent outside the detection zone; in reality, the detection would be more gradated dependent. To identify how important these factors are larger more complex simulations would need to be developed.

5.4.4 Implications for ecology and conservation

The gREM can estimate densities of a number of taxa where no, or few, accurate methods currently exist to measure absolute animal density and trends in absolute abundances (Thomas and Marques, 2012). Many of these species are critically endangered and monitoring their populations is of conservation interest. For example, current methods of density estimation for the threatened Francisana dolphin (*Pontoporia blainvillei*) may result in underestimation of their numbers (Crespo et al., 2010). Our method may also be important for understanding zoonotic diseases; for example, estimating population sizes of echolocating bats, which are an important reservoir of infectious disease that affect humans, livestock and wildlife (Calisher et al., 2006). In addition, using gREM it may be easier to measure the density of animals which may be useful in quantifying ecosystem services, such as studying the levels of songbirds which are known to have a positive influence on pest control in coffee production (Jirinec et al., 2011). The gREM is suitable for any species that would be consistently recorded within range of a detector, such as echolocating bats (Kunz et al., 2009), songbirds (Buckland and Handel, 2006), whales (Marques et al., 2009) or forest primates (Hassel-Finnegan et al., 2008). However some ad-

justments may need to be made for animals who do not make calls frequently, as this model assumes that the taregt species makes constant noise. With increasing technological capabilities, this list of species is likely to increase dramatically. Finally, the passive sensor methods that the gREM use are noninvasive and do not require individual marking (Jewell, 2013) or naturally identifying marks (as required for mark-recapture models). This makes them suitable for large, continuous monitoring projects with limited human resources (Kelly et al., 2012). It also makes them suitable for species that are under pressure, species that cannot naturally be individually recognised or species that are difficult or dangerous to catch (Thomas and Marques, 2012). However, this may not be the most efficient method for species at extremely low densities such as snow leopards.

Chapter 6

General Conclusions

This thesis investigated the methodology behind the estimation of animal density using remote sensors, particularly camera traps. Approximating animal numbers is an important part of animal conservation because it helps in the evaluation of policies used to conserve threatened species. In the uphill struggle to preserve the world's most threatened species, accurate information is vital. However, monitoring that produces systematically biased, imprecise, or misleading results, is not just worthless, it can actually be harmful to conservation (Legg and Nagy, 2006). In addition, without sufficient precision it is not possible to identify changes in density, and therefore running the study is a waste of resources (Nichols and Williams, 2006; Martin et al., 2007). After reviewing the literature Yoccoz et al. (2001) found that a common problem in monitoring studies was a lack of focus on the purpose of the study. For some studies a lack of focus has resulted in either inaccurate or imprecise results, or result in precise estimates for a value that has no relevance to management decisions.

The best possible method for testing density estimation techniques using camera traps would involve a closed system of animals in which no births, deaths or migration could happen without the knowledge of researchers. On top of this, to test the accuracy and the precision of the density estimation techniques a researcher would need: a large amount of funding for cameras and equipment, a huge amount of human effort, and, most of all, the time to create and run the study. Unfortunately, there few environments that come close to that described, and there are rarely suf-

ficient resources to allocate to such a study. Given that a study of this nature is extremely unlikely, it is impossible to know truly whether the density estimation techniques are unbiased when used under field conditions. The best alternative methodology is that used in this thesis, creating a simulation as close to true animal movement as possible, and simulating their movement in a world with camera arrays to test whether the results of the density estimation techniques are credible.

The guidelines about survey design that existed in the literature were quite broad, with the guidelines for CMR being more strict than SECR. There may be more guidelines surrounding the accuracy and precision of CMR results because the methodology is less suited to the real world problem of animal density estimation. This might be partly due to the length of time that CMR has been available for researchers to study; the guidelines for SECR have yet to be developed as fully. Many of the field studies that existed did not reach the minimum threshold suggested by the pre-existing guidelines, detailed in Chapter 2 , which indicated that they may have produced estimates that are not accurate and/or precise. The classification method that was used in this thesis to assess the reliability of studies in terms of some, moderate and strong evidence of bias was not perfect. For example, within the classification system that was setup, the Pampas cat estimate by Caruso et al. (2012) was classified as moderately biased, however it was 10,000 times the size of other density estimates for Pampas cats. This might be because there were a number of factors that were not investigated, such as the effect that animal density has on the guidelines. However, the methodology does attempt to classify the accuracy of density estimation techniques on a much wider range of cat species than have been examined before.

As SECR is becoming the dominant methodology in the field of felid ecology and because, based on these previous studies, it was believed to be easier to design a unbiased study, the SECR model was chosen as the focus for the next part of the thesis. In order to create a realistic simulation of animal movement, the GPS data provided by Tom Mccarthy and his team (McCarthy and Johansson, 2013) was analysed. From this, it was clear that the SECR assumptions about the detection

probability falling off do not match the most commonly used detection functions. In the limit, the invalid assumption did not stop the SECR estimating accurately. However, at lower levels of effort there is a limited range of study designs where SECR produces an unbiased results; the lower the effort, the more at risk of bias. For example, on average around 25 cameras are used in a felid survey, but only when the cameras are set up with an inter-trap distance of 6 km and 7 km, is an unbiased result returned from the SECR model. If we compare to a situation in which 100 cameras are used, a survey design produces reasonable results if the inter trap distance is between 3 km and 9 km.

Given that SECR can easily become biased when average effort is used, gREM was investigated as an alternative density estimation method for snow leopards. Like SECR, the movement of snow leopards also invalidates the assumptions used in gREM; namely that the animals should be randomly moving particles. gREM will produce unbiased results for almost any effort; however, it will result in extremely low levels of precision if enough effort is not used. This will render the result unusable if the number of captures produced is fewer than 60.

The results in this thesis show that there is a need to increase the amount of effort that is applied to studies. This will reduce the chance of poor survey design biasing studies using SECR and will increase the precision for gREM studies. As has previously been suggested by Tobler and Powell (2013), one large comprehensive study would be much preferable to multiple smaller studies. This thesis repeats earlier warnings that models should only be used if they are appropriate when the data has been collected (Foster and Harmsen, 2012).

6.1 Further work

The methodology used in this thesis is by no means perfect; ideally, the next steps for this methodology would be a sensitivity analysis and then further investigation to include additional factors into the simulation, for example topography. This would make the simulation of movement a better representation of real movement and include the additional complexity that makes studying these animals difficult.

However, this is not trivial. The volume of data required for this would potentially be huge, depending on how the additional factors would be modelled. The data received from McCarthy and Johansson (2013) was an excellent dataset but, if more complex movement models are to be run in the future, then a purpose-made data collection would be advisable.

The gREM methodology needs to be tested in the real world. The acoustic modelling has to be tested against other methodologies in the field, preferably in an environment with a relatively understood ecology. There are a number of practical difficulties including calculating the detection angle and the signal width. As was shown, if these angles were miscalculated, then this results in a bias proportional to the size of the miscalculation.

The work in this thesis could be developed further by adding in addition factors into the simulation, such as those outlined in Table 6.1.

6.2 Summary

Researchers already maximise the amount of effort in studies and agonise over study design because they know that they are extremely important factors for the success, or failure, of a study. However, based on the results that were found in this thesis, many of the studies that are published are likely to be biased and have low precision, and this could lead to poor policy being made about conservation and funding for endangered species (Martin et al., 2007; Legg and Nagy, 2006). If the correct methodology is used, with enough sampling effort, then strong inferences can be made about the success or failure of conservation techniques (Rosenblatt et al., 2014; Legg and Nagy, 2006). Therefore those submitting, and considering, research proposals should make sure that enough cameras and effort is being allocated for a study (Foster and Harmsen, 2012).

Change	Discussion
GPS data with high frequency	Higher frequency GPS data could possible identify more movement states and allow for a better simulation of movement. High frequency data would also allow additional factors to be included in the analysis such as time of day.
Calculating distance travelled including change in altitude	It the data analysis in the simulation calculated the movement between locations taking into account the change of gradient movement patterns would be a better reflection of actual movement. This would lead to a more robust movement model and therefore a better understanding of camera placement may be gained in terms of terrain could be gained.
Simulating trails	As many field studies place traps on trails, being able to incorporate trails in the simulation would allow for a better understanding of the impact of these in field work
Behaviour traits	Including behaviour traits, such as trap shyness, which may differ between subpopulations may give interesting feed back as to the effect on sample heterogeneity
Misclassifications	The impact of mis-identifying an animal is not known, this would be a interesting sensitivity analysis
Camera formations	Different grid formations may have a large impact on the accuracy and precision of density estimates. For example it may be worth examining the impact of trying multiple small grid formations, rather than one large grid.
Environmental factor	The landscape, prey and predator locations all play a part in movement, including these in a simulation would increase the reliability of the results.

Table 6.1: Changes to the simulation that would increase it's value

References

Acevedo, M. A. and Villanueva-Rivera, L. J. (2006). Using automated digital recording systems as effective tools for the monitoring of birds and amphibians. *Wildlife Society Bulletin*, 34(1):211–214.

Adams, A., Jantzen, M., Hamilton, R., and Fenton, M. (2012). Do you hear what i hear? Implications of detector selection for acoustic monitoring of bats. *Methods in Ecology and Evolution*.

Ahlen, I. and Baagøe, H. J. (1999). Use of ultrasound detectors for bat studies in Europe: experiences from field identification, surveys, and monitoring. *Acta Chiropterologica*, 1(2):137–150.

Alexander, J. S., Gopalaswamy, A. M., Shi, K., and Riordan, P. (2015). Face value: towards robust estimates of snow leopard densities. *PloS one*, 10(8):e0134815.

Anderson, D. R. (2001). The need to get the basics right in wildlife field studies. *Wildlife Society Bulletin*, 29(4):1294–1297.

Anderson-Sprecher, R. and Ledolter, J. (1991). State-space analysis of wildlife telemetry data. *Journal of the American Statistical Association*, 86(415):596–602.

Anile, S., Bizzarri, L., and Ragni, B. (2010). Estimation of european wildcat population size in sicily (italy) using camera trapping and capture–recapture analyses. *Italian Journal of Zoology*, 77(2):241–246.

Anwar, M. B., Jackson, R., Nadeem, M. S., Janečka, J. E., Hussain, S., Beg, M. A., Muhammad, G., and Qayyum, M. (2011). Food habits of the snow leopard panthera uncia (schreber, 1775) in baltistan, northern pakistan. *European Journal of Wildlife Research*, 57(5):1077–1083.

Auder, B., Lebret, R., Iovleff, S., and Langrognet, F. (2014). *Rmixmod: An interface for MIXMOD*. R package version 2.0.2.

Bagchi, S. and Mishra, C. (2006). Living with large carnivores: predation on livestock by the snow leopard (uncia uncia). *Journal of Zoology*, 268(3):217–224.

Balme, G. A., Hunter, L. T., and Slotow, R. (2009). Evaluating methods for counting cryptic carnivores. *The Journal of wildlife management*, 73(3):433–441.

Barlow, J. and Taylor, B. (2005). Estimates of sperm whale abundance in the northeastern temperate pacific from a combined acoustic and visual survey. *Marine Mammal Science*, 21(3):429–445.

Benhamou, S. and Cornélis, D. (2010). Incorporating movement behavior and barriers to improve kernel home range space use estimates. *Journal of Wildlife Management*, 74(6):1353–1360.

Bjørneraas, K., Mootrer, B., Rolandsen, C. M., and Herfindal, I. (2010). Screening global positioning system location data for errors using animal movement characteristics. *The Journal of Wildlife Management*, 74(6):1361–1366.

Blumstein, D. T., Mennill, D. J., Clemins, P., Girod, L., Yao, K., Patricelli, G., Deppe, J. L., Krakauer, A. H., Clark, C., Cortopassi, K. A., et al. (2011). Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. *Journal of Applied Ecology*, 48(3):758–767.

Bondrup-Nielsen, S. (1983). Density estimation as a function of live-trapping grid and home range size. *Canadian Journal of Zoology*, 61(10):2361–2365.

Borchers, D., Distiller, G., Foster, R., Harmsen, B., and Milazzo, L. (2014). Continuous-time spatially explicit capture–recapture models, with an application to a jaguar camera-trap survey. *Methods in Ecology and Evolution*, 5(7):656–665.

Borchers, D. L. and Efford, M. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, 64(2):377–385.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S., and Coulson, T. (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, 75(6):1393–1405.

Bowler, D. E. and Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, 80(2):205–225.

Bowman, J., Jaeger, J. A., and Fahrig, L. (2002). Dispersal distance of mammals is proportional to home range size. *Ecology*, 83(7):2049–2055.

Brillinger, D. R. (2003). Simulating constrained animal motion using stochastic differential equations. *Lecture Notes-Monograph Series*, pages 35–48.

Brillinger, D. R. and Stewart, B. S. (1998). Elephant-seal movements: Modelling migration. *Canadian Journal of Statistics*, 26(3):431–443.

Brinkløv, S., Jakobsen, L., Ratcliffe, J., Kalko, E., and Surlykke, A. (2011). Echolocation call intensity and directionality in flying short-tailed fruit bats, *Carollia perspicillata* (phyllostomidae). *The Journal of the Acoustical Society of America*, 129(1):427–435.

Brodie, J. and Giordano, A. J. (2012). Density of the vulnerable sunda clouded leopard neofelis diardi in a protected area in sabah, malaysian borneo. *Oryx*, 46(03):427–430.

Brusa, A. and Bunker, D. E. (2014). Increasing the precision of canopy closure estimates from hemispherical photography: Blue channel analysis and under-exposure. *Agricultural and Forest Meteorology*, 195:102–107.

Buckland, S., Newman, K., Thomas, L., and Koesters, N. (2004). State-space models for the dynamics of wild animal populations. *Ecological modelling*, 171(1):157–175.

Buckland, S. T. and Handel, C. (2006). Point-transect surveys for songbirds: robust methodologies. *The Auk*, 123(2):345–357.

Buckland, S. T., Marsden, S. J., and Green, R. E. (2008). Estimating bird abundance: making methods work. *Bird Conservation International*, 18(S1):S91–S108.

Cagnacci, F., Boitani, L., Powell, R. A., and Boyce, M. S. (2010). Animal ecology meets gps-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550):2157–2162.

Calisher, C., Childs, J., Field, H., Holmes, K., and Schountz, T. (2006). Bats: important reservoir hosts of emerging viruses. *Clinical Microbiology Reviews*, 19(3):531–545.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., et al. (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, 4(01):75–79.

Carbone, C., Cowlishaw, G., Isaac, N. J., and Rowcliffe, J. M. (2005). How far do animals go? Determinants of day range in mammals. *The American Naturalist*, 165(2):290–297.

Carroll, C. and Miquelle, D. G. (2006). Spatial viability analysis of amur tiger panthera tigris altaica in the russian far east: the role of protected areas

and landscape matrix in population persistence. *Journal of Applied Ecology*, 43(6):1056–1068.

Caruso, N., Manfredi, C., Vidal, E. M. L., Casanaveo, E. B., and Lucherinio, M. (2012). First density estimation of two sympatric small cats, leopardus colocolo and leopardus geoffroyi, in a shrubland area of central argentina. In *Annales Zoologici Fennici*, volume 49, pages 181–191. BioOne.

Caughley, G. and Sinclair, A. R. E. (1994). *Wildlife ecology and management*. Blackwell Science.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., and Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, 1(5):e1400253.

Chandler, R. B., Royle, J. A., et al. (2013). Spatially explicit models for inference about density in unmarked or partially marked populations. *The Annals of Applied Statistics*, 7(2):936–954.

Clark, C. W. (1995). Application of US Navy underwater hydrophone arrays for scientific research on whales. *Reports of the International Whaling Commission*, 45:210–212.

Costanza, R., d'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'neill, R. V., Paruelo, J., et al. (1998). The value of the world's ecosystem services and natural capital. *Ecological economics*, 1(25):3–15.

Crespo, E. A., Pedraza, S. N., Grandi, M. F., Dans, S. L., and Garaffo, G. V. (2010). Abundance and distribution of endangered Franciscana dolphins in Argentine waters and conservation implications. *Marine Mammal Science*, 26(1):17–35.

Cutler, T. L. and Swann, D. E. (1999). Using remote photography in wildlife ecology: a review. *Wildlife Society Bulletin*, 27(3):571–581.

Damuth, J. (1981). Population density and body size in mammals. *Nature*, 290(5808):699–700.

Davis, R., Fuiman, L., Williams, T., Collier, S., Hagey, W., Kanatous, S., Kohin, S., and Horning, M. (1999). Hunting behavior of a marine mammal beneath the antarctic fast ice. *Science*, 283(5404):993–996.

de la Torre, J. A. and Medellín, R. A. (2011). Jaguars panthera onca in the greater lacandona ecosystem, chiapas, mexico: population estimates and future prospects. *Oryx*, 45(04):546–553.

D'Eon, R. G., Serrouya, R., Smith, G., and Kochanny, C. O. (2002). Gps radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin*, pages 430–439.

D'Eon, Robert G, R. G. and Delparte, D. (2005). Effects of radio-collar position and orientation on gps radio-collar performance, and the implications of pdop in data screening. *Journal of Applied Ecology*, 42(2):383–388.

Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S., and Sueur, J. (2012). Monitoring animal diversity using acoustic indices: implementation in a temperate woodland. *Ecological Indicators*, 13(1):46–54.

Di Bitetti, M. S., Paviolo, A., De Angelo, C. D., and Di Blanco, Y. E. (2008). Local and continental correlates of the abundance of a neotropical cat, the ocelot (leopardus pardalis). *Journal of Tropical Ecology*, 24(02):189–200.

Di Orio, A. P., Callas, R., and Schaefer, R. J. (2003). Performance of two gps telemetry collars under different habitat conditions. *Wildlife Society Bulletin*, pages 372–379.

Dillon, A. and Kelly, M. (2008). Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. *Journal of Zoology*, 275(4):391–398.

Dussault, C., Courtois, R., Ouellet, J.-P., and Huot, J. (2001). Influence of satellite geometry and differential correction on gps location accuracy. *Wildlife Society Bulletin*, pages 171–179.

Efford, M. (2004). Density estimation in live-trapping studies. *Oikos*, 106(3):598–610.

Efford, M. (2015). *secr: Spatially explicit capture-recapture models, R package version 2.9.5*.

Efford, M. G. (2011). Estimation of population density by spatially explicit capture-recapture analysis of data from area searches. *Ecology*, 92(12):2202–2207.

Efford, M. G. (2014). Bias from heterogeneous usage of space in spatially explicit capture–recapture analyses. *Methods in Ecology and Evolution*, 5(7):599–602.

Efford, M. G., Borchers, D. L., and Byrom, A. E. (2009). Density estimation by spatially explicit capture–recapture: likelihood-based methods. In *Modeling demographic processes in marked populations*, pages 255–269. Springer.

Efford, M. G. and Fewster, R. M. (2013). Estimating population size by spatially explicit capture–recapture. *Oikos*, 122(6):918–928.

Elphick, C. S. (2008). How you count counts: the importance of methods research in applied ecology. *Journal of Applied Ecology*, 45(5):1313–1320.

Everatt, K. T., Andresen, L., and Somers, M. J. (2014). Trophic scaling and occupancy analysis reveals a lion population limited by top-down anthropogenic pressure in the Limpopo National Park, Mozambique. *PloS one*, 9(6):e99389.

Foster, R. J. and Harmsen, B. J. (2012). A critique of density estimation from camera-trap data. *The Journal of Wildlife Management*, 76(2):224–236.

Frair, J. L., Nielsen, S. E., Merrill, E. H., Lele, S. R., Boyce, M. S., Munro, R. H., Stenhouse, G. B., and Beyer, H. L. (2004). Removing gps collar bias in habitat selection studies. *Journal of Applied Ecology*, 41(2):201–212.

Fraley, C., Raftery, A. E., Murphy, T. B., and Scrucca, L. (2012). *mclust Version 4 for R: Normal Mixture Modeling for Model-Based Clustering, Classification, and Density Estimation*. Department of Statistics, University of Washington.

Franke, A., Caelli, T., and Hudson, R. J. (2004). Analysis of movements and behavior of caribou (¡ i¿ rangifer tarandus¡/i¿) using hidden markov models. *Ecological Modelling*, 173(2):259–270.

Fusco-Costa, R., Ingberman, B., do Couto, H. T. Z., Nakano-Oliveira, E., and de Araujo Monteiro-Filho, E. L. (2010). Population density of a coastal island population of the ocelot in atlantic forest, southeastern brazil. *Mammalian Biology-Zeitschrift für Säugetierkunde*, 75(4):358–362.

Ganskopp, D. C. and Johnson, D. D. (2007). Gps error in studies addressing animal movements and activities. *Rangeland Ecology & Management*, 60(4):350–358.

Gardner, B., Reppucci, J., Lucherini, M., and Royle, J. A. (2010a). Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. *Ecology*, 91(11):3376–3383.

Gardner, B., Royle, J. A., Wegan, M. T., Rainbolt, R. E., and Curtis, P. D. (2010b). Estimating black bear density using dna data from hair snares. *The Journal of Wildlife Management*, 74(2):318–325.

Garrote, G., De Ayala, R. P., Pereira, P., Robles, F., Guzman, N., García, F. J., Iglesias, M. C., Hervás, J., Fajardo, I., Simón, M., et al. (2011). Estimation of the iberian lynx (lynx pardinus) population in the doñana area, sw spain, using capture–recapture analysis of camera-trapping data. *european Journal of wildlife Research*, 57(2):355–362.

Garrote, G., Gil-Sánchez, J. M., McCain, E. B., de Lillo, S., Tellería, J. L., and Simón, M. Á. (2012). The effect of attractant lures in camera trapping: a case study of population estimates for the iberian lynx (lynx pardinus). *European journal of wildlife research*, 58(5):881–884.

Ghoddousi, A., Hamidi, A. H. K., Ghadirian, T., Ashayeri, T., Moshiri, H., and Khorozyan, I. (2008). The status of the persian leopard in bamu national park, iran. *Cat News*, 49:10–13.

Gil-Sánchez, J. M., Moral, M., Bueno, J., Rodríguez-Siles, J., Lillo, S., Pérez, J., Martín, J. M., Valenzuela, G., Garrote, G., Torralba, B., et al. (2011). The use of camera trapping for estimating iberian lynx (lynx pardinus) home ranges. *European journal of wildlife research*, 57(6):1203–1211.

Girard, I., Ouellet, J.-P., Courtois, R., Dussault, C., and Breton, L. (2002). Effects of sampling effort based on gps telemetry on home-range size estimations. *The Journal of wildlife management*, pages 1290–1300.

Gitzen, R. A., Millspaugh, J. J., and Kernohan, B. J. (2006). Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *Journal of Wildlife Management*, 70(5):1334–1344.

González-Maya, J. F. and Cardenal-Porras, J. (2012). Ocelot density in the caribbean slope of the talamanca region, costa rica. *Hystrix, the Italian Journal of Mammalogy*, 22(2).

Gopalaswamy, A. M., Delampady, M., Karanth, K. U., Kumar, N., and Macdonald, D. W. (2015). An examination of index-calibration experiments: counting tigers at macroecological scales. *Methods in Ecology and Evolution*.

Gopalaswamy, A. M., Royle, J. A., Delampady, M., Nichols, J. D., Karanth, K. U., and Macdonald, D. W. (2012). Density estimation in tiger populations: combining information for strong inference. *Ecology*, 93(7):1741–1751.

Gopi, S. (2005). *Global positioning System: Principles and applications*. Tata McGraw-Hill Education.

Graves, T. A. and Waller, J. S. (2006). Understanding the causes of missed global positioning system telemetry fixes. *Journal of Wildlife Management*, 70(3):844–851.

Gray, T. N. (2012). Studying large mammals with imperfect detection: status and habitat preferences of wild cattle and large carnivores in eastern cambodia. *Biotropica*, 44(4):531–536.

Gray, T. N. E. and Prum, S. (2012). Leopard density in post-conflict landscape, cambodia: Evidence from spatially explicit capture–recapture. *The Journal of Wildlife Management*, 76(1):163–169.

Guil, F., Agudín, S., El-Khadir, N., Fernandez-Olalla, M., Figueredo, J., Domínguez, F. G., Garzon, P., Gonzalez, G., Muñoz-Igualada, J., Oria, J., et al. (2010). Factors conditioning the camera-trapping efficiency for the iberian lynx (lynx pardinus). *European journal of wildlife research*, 56(4):633–640.

Harihar, A., Pandav, B., and Goyal, S. P. (2009a). Density of leopards (panthera pardus) in the chilla range of rajaji national park, uttarakhand, india. *Mammalia*, 73(1):68–71.

Harihar, A., Pandav, B., and Goyal, S. P. (2009b). Responses of tiger (panthera tigris) and their prey to removal of anthropogenic influences in rajaji national park, india. *European Journal of Wildlife Research*, 55(2):97–105.

Harihar, A., Pandav, B., and Goyal, S. P. (2011). Responses of leopard panthera pardus to the recovery of a tiger panthera tigris population. *Journal of Applied Ecology*, 48(3):806–814.

Harihar, A., Prasad, D. L., Ri, C., Pandav, B., and Goyal, S. P. (2009c). Losing ground: tigers panthera tigris in the north-western shivalik landscape of india. *Oryx*, 43(01):35–43.

Harmsen, B. J., Foster, R. J., and Doncaster, C. P. (2011). Heterogeneous capture rates in low density populations and consequences for capture-recapture analysis of camera-trap data. *Population Ecology*, 53(1):253–259.

Harris, D., Matias, L., Thomas, L., Harwood, J., and Geissler, W. H. (2013). Applying distance sampling to fin whale calls recorded by single seismic instruments

in the northeast Atlantic. *The Journal of the Acoustical Society of America*, 134(5):3522–3535.

Harris, R. and Reading, R. (2008). Ovis ammon. the iucn red list of threatened species 2008: e.t15733a5074694.

Hassel-Finnegan, H. M., Borries, C., Larney, E., Umponjan, M., and Koenig, A. (2008). How reliable are density estimates for diurnal primates? *International Journal of Primatology*, 29(5):1175–1187.

Hayes, J. P. (2000). Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. *Acta Chiropterologica*, 2(2):225–236.

Hebblewhite, M. and Haydon, D. T. (2010). Distinguishing technology from biology: a critical review of the use of gps telemetry data in ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550):2303–2312.

Hemmer, H. (1972). Uncia uncia. *Mammalian Species*, (20):1–5.

Heptner, V. G. (1992). *Mammals of the Soviet Union, Volume 2 Part 2 Carnivora (Hyenas and Cats)*, volume 2. Brill.

Holderied, M. and Von Helversen, O. (2003). Echolocation range and wingbeat period match in aerial-hawking bats. *Proc. R. Soc. B*, 270(1530):2293–2299.

Hurford, A. (2009). Gps measurement error gives rise to spurious 180 turning angles and strong directional biases in animal movement data. *PloS one*, 4(5):e5632.

Hutchinson, J. M. C. and Waser, P. M. (2007). Use, misuse and extensions of "ideal gas" models of animal encounter. *Biological Reviews of the Cambridge Philosophical Society*, 82(3):335–359.

IUCN (2012). The iucn red list of threatened species. `http://www.iucnredlist.org/`.

IUCN (2015). *The IUCN Red List of Threatened Species. Version 2015-4.*

Ivan, J. S., White, G. C., and Shenk, T. M. (2013). Using simulation to compare methods for estimating density from capture-recapture data. *Ecology*, 94(4):817–826.

Jackson, R. and Ahlborn, G. (1989). Snow leopards (panthera uncia) in nepal: home range and movements. *National Geographic Research*, 5(2):161–175.

Jackson, R., Mallon, D., McCarthy, T., Chundaway, R., and Habib, B. (2008). Panthera uncia. the iucn red list of threatened species. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T22732A9381126.en.

Jackson, R., Munkhtsog, B., Mallon, D., Naranbaatar, G., and Gerelmaa, K. (2009). Camera-trapping snow leopards in the tost uul region of mongolia. *Cat News*, 51:18–21.

Jackson, R. M. (1996). *Home range, movements and habitat use of snow leopard(Uncia uncia) in Nepal*. PhD thesis, University of London London, United Kingdom.

Jackson, R. M., Roe, J. D., Wangchuk, R., and Hunter, D. O. (2006). Estimating snow leopard population abundance using photography and capture-recapture techniques. *Wildlife Society Bulletin*, 34(3):772–781.

Janečka, J. E., Munkhtsog, B., Jackson, R. M., Naranbaatar, G., Mallon, D. P., and Murphy, W. J. (2011). Comparison of noninvasive genetic and camera-trapping techniques for surveying snow leopards. *Journal of Mammalogy*, 92(4):771–783.

Janis, C. M. and Wilhelm, P. B. (1993). Were there mammalian pursuit predators in the tertiary? dances with wolf avatars. *Journal of Mammalian Evolution*, 1(2):103–125.

Jerde, C. L. and Visscher, D. R. (2005). Gps measurement error influences on movement model parameterization. *Ecological Applications*, 15(3):806–810.

Jewell, Z. (2013). Effect of monitoring technique on quality of conservation science. *Conservation Biology*, 27(3):501–508.

Jirinec, V., Campos, B. R., and Johnson, M. D. (2011). Roosting behaviour of a migratory songbird on Jamaican coffee farms: landscape composition may affect delivery of an ecosystem service. *Bird Conservation International*, 21(03):353–361.

Johansson, Ö., McCarthy, T., Samelius, G., Andrén, H., Tumursukh, L., and Mishra, C. (2015). Snow leopard predation in a livestock dominated landscape in mongolia. *Biological Conservation*, 184:251–258.

Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., Teacher, A., Bininda-Emonds, O. R. P., Gittleman, J. L., Mace, G. M., Purvis, A., and Michener, W. K. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90(9):2648.

Jones, K. E., Russ, J. A., Bashta, A.-T., Bilhari, Z., Catto, C., Csősz, I., Gorbachev, A., Győrfi, P., Hughes, A., Ivashkiv, I., Koryagina, N., Kurali, A., Langton, S., Collen, A., Margiean, G., Pandourski, I., Parsons, S., Prokofev, I., Szodoray-Paradi, A., Szodoray-Paradi, F., Tilova, E., Walters, C. L., Weatherill, A., and Zavarzin, O. (2013). Indicator bats program: A system for the global acoustic monitoring of bats. In Collen, B., Pettorelli, N., Baillie, J. E. M., and Durant, S. M., editors, *Biodiversity Monitoring and Conservation*, pages 211–247. Wiley-Blackwell.

Jonsen, I. D., Flemming, J. M., and Myers, R. A. (2005). Robust state-space modeling of animal movement data. *Ecology*, 86(11):2874–2880.

Jonsen, I. D., Myers, R. A., and Flemming, J. M. (2003). Meta-analysis of animal movement using state-space models. *Ecology*, 84(11):3055–3063.

Kalle, R., Ramesh, T., Qureshi, Q., and Sankar, K. (2011). Density of tiger and leopard in a tropical deciduous forest of mudumalai tiger reserve, southern india, as estimated using photographic capture–recapture sampling. *Acta Theriologica*, 56(4):335–342.

Karanth, K. U. (1995). Estimating tiger panthera tigris populations from camera-trap data using capture—recapture models. *Biological conservation*, 71(3):333–338.

Karanth, K. U., Gopalaswamy, A. M., Kumar, N. S., Vaidyanathan, S., Nichols, J. D., and MacKenzie, D. I. (2011). Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. *Journal of Applied Ecology*, 48(4):1048–1056.

Karanth, K. U. and Nichols, J. D. (1998). Estimation of tiger densities in india using photographic captures and recaptures. *Ecology*, 79(8):2852–2862.

Karanth, K. U. and Sunquist, M. E. (2000). Behavioural correlates of predation by tiger (panthera tigris), leopard (panthera pardus) and dhole (cuon alpinus) in nagarahole, india. *Journal of Zoology*, 250(02):255–265.

Kays, R., Kranstauber, B., Jansen, P., Carbone, C., Rowcliffe, M., Fountain, T., and Tilak, S. (2009). Camera traps as sensor networks for monitoring animal communities. In *Local Computer Networks, 2009. LCN 2009. IEEE 34th Conference on*, pages 811–818. IEEE.

Kelly, M. J. (2008). Design, evaluate, refine: camera trap studies for elusive species. *Animal Conservation*, 11(3):182–184.

Kelly, M. J., Betsch, J., Wultsch, C., Mesa, B., and Mills, L. S. (2012). Noninvasive sampling for carnivores. In Boitani, L. and Powell, R., editors, *Carnivore*

ecology and conservation: a handbook of techniques, pages 47–69. Oxford University Press, New York.

Kelly, M. J. and Holub, E. L. (2008). Camera trapping of carnivores: trap success among camera types and across species, and habitat selection by species, on salt pond mountain, giles county, virginia. *Northeastern Naturalist*, 15(2):249–262.

Kelly, M. J., Noss, A. J., Di Bitetti, M. S., Maffei, L., Arispe, R. L., Paviolo, A., De Angelo, C. D., and Di Blanco, Y. E. (2008). Estimating puma densities from camera trapping across three study sites: Bolivia, argentina, and belize. *Journal of Mammalogy*, 89(2):408–418.

Kelt, D. A. and Van Vuren, D. H. (2001). The ecology and macroecology of mammalian home range area. *The American Naturalist*, 157(6):637–645.

Kessel, S., Cooke, S., Heupel, M., Hussey, N., Simpfendorfer, C., Vagle, S., and Fisk, A. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries*, 24(1):199–218.

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., Gaillard, J.-M., and Moorcroft, P. R. (2010). The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365(1550):2221–2231.

Kimura, S., Akamatsu, T., Dong, L., Wang, K., Wang, D., Shibata, Y., and Arai, N. (2014). Acoustic capture-recapture method for towed acoustic surveys of echolocating porpoises. *The Journal of the Acoustical Society of America*, 135(6):3364–3370.

Knape, J. and de Valpine, P. (2012). Are patterns of density dependence in the global population dynamics database driven by uncertainty about population abundance? *Ecology letters*, 15(1):17–23.

Kolowski, J. and Alonso, A. (2010). Density and activity patterns of ocelots (leopardus pardalis) in northern peru and the impact of oil exploration activities. *Biological Conservation*, 143(4):917–925.

Kunz, T. H., Betke, M., Hristov, N. I., and Vonhof, M. (2009). Methods for assessing colony size, population size, and relative abundance of bats. In Kunz, T. and Parsons, S., editors, *Ecological and behavioral methods for the study of bats*, pages 133–157. Johns Hopkins University Press, Baltimore, Maryland, 2nd edition.

Lammers, M. O. and Au, W. W. (2003). Directionality in the whistles of Hawaiian spinner dolphins (*Stenella longirostris*): A signal feature to cue direction of movement? *Marine Mammal Science*, 19(2):249–264.

Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., and Morales, J. M. (2012). Flexible and practical modeling of animal telemetry data: hidden markov models and extensions. *Ecology*, 93(11):2336–2342.

Laube, P. and Purves, R. S. (2011). How fast is a cow? cross-scale analysis of movement data. *Transactions in GIS*, 15(3):401–418.

Legg, C. J. and Nagy, L. (2006). Why most conservation monitoring is, but need not be, a waste of time. *Journal of environmental management*, 78(2):194–199.

Lewis, J. S., Rachlow, J. L., Garton, E. O., and Vierling, L. A. (2007a). Effects of habitat on gps collar performance: using data screening to reduce location error. *Journal of Applied Ecology*, 44(3):663–671.

Lewis, T., Gillespie, D., Lacey, C., Matthews, J., Danbolt, M., Leaper, R., McLanaghan, R., and Moscrop, A. (2007b). Sperm whale abundance estimates from acoustic surveys of the Ionian Sea and Straits of Sicily in 2003. *Journal of the Marine Biological Association of the United Kingdom*, 87(01):353–357.

Li, J. and Lu, Z. (2014). Snow leopard poaching and trade in china 2000–2013. *Biological Conservation*, 176:207–211.

Lindberg, M. S. and Walker, J. (2007). Satellite telemetry in avian research and management: sample size considerations. *The Journal of wildlife management*, 71(3):1002–1009.

Lindenmayer, D. B. and Likens, G. E. (2010). The science and application of ecological monitoring. *Biological Conservation*, 143(6):1317–1328.

Linkie, M., Guillera-Arroita, G., Smith, J., and Rayan, D. M. (2010). Monitoring tigers with confidence. *Integr Zool*, 5:342–350.

López-Parra, M., Fernández, L., Ruiz, G., Gil-Sánchez, J. M., Simón, M. A., López, G., and Sarmento, P. (2012). Change in demographic patterns of the doñana iberian lynx lynx pardinus: management implications and conservation perspectives. *Oryx*, 46(03):403–413.

Lucas, T. C., Moorcroft, E. A., Freeman, R., Rowcliffe, J. M., and Jones, K. E. (2015). A generalised random encounter model for estimating animal density with remote sensor data. *Methods in Ecology and Evolution*, 6(5):500–509.

Lynam, A. J., Rabinowitz, A., Myint, T., Maung, M., Latt, K. T., and Po, S. H. T. (2009). Estimating abundance with sparse data: tigers in northern myanmar. *Population Ecology*, 51(1):115–121.

MacKenzie, D. I. and Royle, J. A. (2005). Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology*, 42(6):1105–1114.

Maffei, L. and Noss, A. J. (2008). How small is too small? camera trap survey areas and density estimates for ocelots in the bolivian chaco. *Biotropica*, 40(1):71–75.

Male, T. D. and Bean, M. J. (2005). Measuring progress in us endangered species conservation. *Ecology Letters*, 8(9):986–992.

Manzo, E., Bartolommei, P., Rowcliffe, J. M., and Cozzolino, R. (2012). Estimation of population density of European pine marten in central Italy using camera trapping. *Acta Theriologica*, 57(2):165–172.

Marcoux, M., Auger-Méthé, M., Chmelnitsky, E. G., Ferguson, S. H., and Humphries, M. M. (2011). Local passive acoustic monitoring of narwhal presence in the Canadian Arctic: a pilot project. *Arctic*, 64(3):307–316.

Marnewick, K., Funston, P. J., and Karanth, K. U. (2008). Evaluating camera trapping as a method for estimating cheetah abundance in ranching areas. *South African Journal of Wildlife Research*, 38(1):59–65.

Marques, T. A., Munger, L., Thomas, L., Wiggins, S., and Hildebrand, J. A. (2011a). Estimating North Pacific right whale (*Eubalaena japonica*) density using passive acoustic cue counting. *Endangered Species Research*, 13(3):163–172.

Marques, T. A., Thomas, L., Martin, S. W., Mellinger, D. K., Ward, J. A., Moretti, D. J., Harris, D., and Tyack, P. L. (2013). Estimating animal population density using passive acoustics. *Biological Reviews*, 88(2):287–309.

Marques, T. A., Thomas, L., and Royle, J. A. (2011b). A hierarchical model for spatial capture-recapture data: comment. *Ecology*, 92(2):526–528.

Marques, T. A., Thomas, L., Ward, J., DiMarzio, N., and Tyack, P. L. (2009). Estimating cetacean population density using fixed passive acoustic sensors: An example with Blainville's beaked whales. *The Journal of the Acoustical Society of America*, 125(4):1982–1994.

Martin, J., Kitchens, W. M., and Hines, J. E. (2007). Importance of well-designed monitoring programs for the conservation of endangered species: Case study of the snail kite. *Conservation Biology*, 21(2):472–481.

McCarthy, J. L., McCarthy, K. P., Fuller, T. K., and McCarthy, T. M. (2010). Assessing variation in wildlife biodiversity in the tien shan mountains of kyrgyzs-

tan using ancillary camera-trap photos. *Mountain Research and Development*, 30(3):295–301.

McCarthy, K. P., Fuller, T. K., Ming, M., McCarthy, T. M., Waits, L., and Jumabaev, K. (2008). Assessing estimators of snow leopard abundance. *The Journal of Wildlife Management*, 72(8):1826–1833.

McCarthy, T. M., Chapron, G., and Network, S. L. (2003). *Snow leopard survival strategy*. International Snow Leopard Trust Seattle, Washington.

McCarthy, T. M., Fuller, T. K., and Munkhtsog, B. (2005). Movements and activities of snow leopards in southwestern mongolia. *Biological Conservation*, 124(4):527–537.

McCarthy, T. M. and Johansson, O. (2013). Snow leopard gps data. "personal communication".

Meek, P., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'Brien, T., O'Connell, A., Sanderson, J., Swann, D., Tobler, M., et al. (2014). Recommended guiding principles for reporting on camera trapping research. *Biodiversity and conservation*, 23(9):2321–2343.

Mills, K. J., Patterson, B. R., Murray, D. L., and Bowman, J. (2006). Effects of variable sampling frequencies on gps transmitter efficiency and estimated wolf home range size and movement distance. *Wildlife Society Bulletin*, 34(5):1463–1469.

Mishra, C., Allen, P., McCarthy, T., Madhusudan, M., Bayarjargal, A., and Prins, H. H. (2003). The role of incentive programs in conserving the snow leopard. *Conservation Biology*, 17(6):1512–1520.

Mishra, C., Prins, H. H., and Wieren, S. E. v. (2001). Overstocking in the trans-himalayan rangelands of india. *Environmental Conservation*, 28(03):279–283.

Moen, R., Pastor, J., Cohen, Y., and Schwartz, C. C. (1996). Effects of moose movement and habitat use on gps collar performance. *The Journal of wildlife management*, pages 659–668.

Monterroso, P., Brito, J., Ferreras, P., and Alves, P. (2009). Spatial ecology of the european wildcat in a mediterranean ecosystem: dealing with small radio-tracking datasets in species conservation. *Journal of Zoology*, 279(1):27–35.

Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E., and Fryxell, J. M. (2004). Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, 85(9):2436–2445.

Musiani, M., Okarma, H., and Jedrzejewski, W. (1998). Speed and actual distances travelled by radiocollared wolves in białowieża primeval forest (poland). *Acta Theriologica*, 43(4):409–416.

Negrões, N., Sarmento, P., Cruz, J., Eira, C., Revilla, E., Fonseca, C., Sollmann, R., TǑRRES, N. M., Furtado, M. M., Jácomo, A. T., et al. (2010). Use of camera-trapping to estimate puma density and influencing factors in central brazil. *The Journal of Wildlife Management*, 74(6):1195–1203.

Negroes, N., Sollmann, R., Fonseca, C., Jacomo, A. T., Revilla, E., and Silveira, L. (2012). One or two cameras per station? monitoring jaguars and other mammals in the amazon. *Ecological research*, 27(3):639–648.

Network, S. L. (2014). Snow leopard survival strategy. *Seattle, Washington, USA*, pages 1–145.

Nichols, J. D. and Williams, B. K. (2006). Monitoring for conservation. *Trends in Ecology & Evolution*, 21(12):668–673.

Noss, A., Gardner, B., Maffei, L., Cuéllar, E., Montaño, R., Romero-Muñoz, A., Sollman, R., and O'Connell, A. (2012). Comparison of density estimation methods for mammal populations with camera traps in the kaa-iya del gran chaco landscape. *Animal Conservation*, 15(5):527–535.

Núñez-Pérez, R. (2011). Estimating jaguar population density using camera-traps: a comparison with radio-telemetry estimates. *Journal of Zoology*, 285(1):39–45.

O'Brien, S. J. and Johnson, W. E. (2007). The evolution cats. *Scientific American*, 297(1):68–75.

O'Brien, T. G., Kinnaird, M. F., and Wibisono, H. T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, 6(2):131–139.

Oli, M. K. (1994). Snow leopards and blue sheep in nepal: densities and predator: prey ratio. *Journal of Mammalogy*, 75(4):998–1004.

Otis, D. L., Burnham, K. P., White, G. C., and Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife monographs*, pages 3–135.

Otis, D. L. and White, G. C. (1999). Autocorrelation of location estimates and the analysis of radiotracking data. *The Journal of Wildlife Management*, pages 1039–1044.

Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O., and Matthiopoulos, J. (2008). State–space models of individual animal movement. *Trends in ecology & evolution*, 23(2):87–94.

Paviolo, A., De Angelo, C. D., Di Blanco, Y. E., and Di Bitetti, M. S. (2008). Jaguar panthera onca population decline in the upper paraná atlantic forest of argentina and brazil. *Oryx*, 42(04):554–561.

Paviolo, A., Di Blanco, Y. E., De Angelo, C. D., and Di Bitetti, M. S. (2009). Protection affects the abundance and activity patterns of pumas in the atlantic forest. *Journal of Mammalogy*, 90(4):926–934.

Pereira, J. A., Fracassi, N. G., and Uhart, M. M. (2006). Numerical and spatial responses of geoffroy's cat (oncifelis geoffroyi) to prey decline in argentina. *Journal of Mammalogy*, 87(6):1132–1139.

Piper, J. (1987). The effect of zero feature correlation assumption on maximum likelihood based classification of chromosomes. *Signal processing*, 12(1):49–57.

Preisler, H. K., Ager, A. A., Johnson, B. K., and Kie, J. G. (2004). Modeling animal movements using stochastic differential equations. *Environmetrics*, 15(7):643–657.

Proctor, M., McLellan, B., Boulanger, J., Apps, C., Stenhouse, G., Paetkau, D., and Mowat, G. (2010). Ecological investigations of grizzly bears in Canada using DNA from hair, 1995-2005: a review of methods and progress. *Ursus*, 21(2):169–188.

Purvis, A., Gittleman, J. L., Cowlishaw, G., and Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1456):1947–1952.

R Core Team (2014). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ramesh, T., Sridharan, N., Sankar, K., Qureshi, Q., Selvan, K. M., Gokulakkannan, N., Francis, P., Narasimmarajan, K., Jhala, Y. V., and Gopal, R. (2012). Status of large carnivores and their prey in tropical rainforests of south-western ghats, india. *Tropical Ecology*, 53(2):137–148.

Rayan, D. M. and Mohamad, S. W. (2009). The importance of selectively logged forests for tiger panthera tigris conservation: a population density estimate in peninsular malaysia. *Oryx*, 43(01):48–51.

Reich, B. J. and Gardner, B. (2014). A spatial capture-recapture model for territorial species. *Environmetrics*, 25(8):630–637.

Rempel, R. S. and Rodgers, A. R. (1997). Effects of differential correction on accuracy of a gps animal location system. *The Journal of Wildlife Management*, pages 525–530.

Rempel, R. S., Rodgers, A. R., and Abraham, K. F. (1995). Performance of a gps animal location system under boreal forest canopy. *The Journal of wildlife management*, pages 543–551.

Reppucci, J., Gardner, B., and Lucherini, M. (2011). Estimating detection and density of the andean cat in the high andes. *Journal of Mammalogy*, 92(1):140–147.

Reuters, T. (2012). Web of science. `http://apps.webofknowledge.com/`.

Richter-Dyn, N. and Goel, N. S. (1972). On the extinction of a colonizing species. *Theoretical Population Biology*, 3(4):406–433.

Riordan, P., Cushman, S. A., Mallon, D., Shi, K., and Hughes, J. (2015). Predicting global population connectivity and targeting conservation action for snow leopard across its range. *Ecography*.

Rogers, T. L., Ciaglia, M. B., Klinck, H., and Southwell, C. (2013). Density can be misleading for low-density species: benefits of passive acoustic monitoring. *Public Library of Science One*, 8(1):e52542.

Rosenblatt, E., Becker, M. S., Creel, S., Droge, E., Mweetwa, T., Schuette, P. A., Watson, F., Merkle, J., and Mwape, H. (2014). Detecting declines of apex carnivores and evaluating their causes: An example with zambian lions. *Biological Conservation*, 180:176–186.

Rovero, F., Zimmermann, F., Berzi, D., and Meek, P. (2013). " which camera trap type and how many do i need?" a review of camera features and study designs for a range of wildlife research applications. *Hystrix, the Italian Journal of Mammalogy*, 24(2):148–156.

Rowcliffe, J., Field, J., Turvey, S., and Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 45(4):1228–1236.

Rowcliffe, J. M. and Carbone, C. (2008). Surveys using camera traps: are we looking to a brighter future? *Animal Conservation*, 11(3):185–186.

Rowcliffe, M. J., Carbone, C., Jansen, P. A., Kays, R., and Kranstauber, B. (2011). Quantifying the sensitivity of camera traps: an adapted distance sampling approach. *Methods in Ecology and Evolution*, 2(5):464–476.

Royle, J. A., Chandler, R. B., Gazenski, K. D., and Graves, T. A. (2013a). Spatial capture-recapture models for jointly estimating population density and landscape connectivity. *Ecology*, 94(2):287–294.

Royle, J. A., Chandler, R. B., Sun, C. C., and Fuller, A. K. (2013b). Integrating resource selection information with spatial capture–recapture. *Methods in Ecology and Evolution*, 4(6):520–530.

Royle, J. A., Chandler, R. B., Sun, C. C., and Fuller, A. K. (2014). Reply to efford on 'integrating resource selection information with spatial capture–recapture'. *Methods in Ecology and Evolution*, 5(7):603–605.

Royle, J. A. and Converse, S. J. (2014). Hierarchical spatial capture–recapture models: modelling population density in stratified populations. *Methods in Ecology and Evolution*, 5(1):37–43.

Royle, J. A., Karanth, K. U., Gopalaswamy, A. M., and Kumar, N. S. (2009a). Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology*, 90(11):3233–3244.

Royle, J. A., Magoun, A. J., Gardner, B., Valkenburg, P., and Lowell, R. E. (2011). Density estimation in a wolverine population using spatial capture–recapture models. *The Journal of wildlife management*, 75(3):604–611.

Royle, J. A. and Nichols, J. D. (2003). Estimating abundance from repeated presence-absence data or point counts. *Ecology*, 84(3):777–790.

Royle, J. A., Nichols, J. D., Karanth, K. U., and Gopalaswamy, A. M. (2009b). A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology*, 46(1):118–127.

Royle, J. A., Sutherland, C., Fuller, A. K., and Sun, C. C. (2015). Likelihood analysis of spatial capture-recapture models for stratified or class structured populations. *Ecosphere*, 6(2):art22.

Royle, J. A. and Young, K. V. (2008). A hierarchical model for spatial capture-recapture data. *Ecology*, 89(8):2281–2289.

Sandell, M. (1989). The mating tactics and spacing patterns of solitary carnivores. In *Carnivore behavior, ecology, and evolution*, pages 164–182. Springer.

Sathyakumar, S., Bashir, T., Bhattacharya, T., and Poudyal, K. (2011). Assessing mammal distribution and abundance in intricate eastern himalayan habitats of khangchendzonga, sikkim, india. *Mammalia*, 75(3):257–268.

Schlägel, U. E. and Lewis, M. A. (2014). Detecting effects of spatial memory and dynamic information on animal movement decisions. *Methods in Ecology and Evolution*, 5(11):1236–1246.

Schmidt, B. R. (2003). Count data, detection probabilities, and the demography, dynamics, distribution, and decline of amphibians. *Comptes Rendus Biologies*, 326:119–124.

Scognamillo, D., Maxit, I. E., Sunquist, M., and Polisar, J. (2003). Coexistence of jaguar (panthera onca) and puma (puma concolor) in a mosaic landscape in the venezuelan llanos. *Journal of Zoology*, 259(03):269–279.

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J., and Gitzen, R. A. (1999). Effects of sample size on kernel home range estimates. *The journal of wildlife management*, pages 739–747.

Sharma, R., Jhala, Y., Qureshi, Q., Vattakaven, J., Gopal, R., and Nayak, K. (2010). Evaluating capture–recapture population and density estimation of tigers in a population with known parameters. *Animal Conservation*, 13(1):94–103.

Shehzad, W., McCarthy, T. M., Pompanon, F., Purevjav, L., Coissac, E., Riaz, T., and Taberlet, P. (2012). Prey preference of snow leopard (panthera uncia) in south gobi, mongolia. *PloS one*, 7(2):e32104.

Silveira, L., Jácomo, A. T., Astete, S., Sollmann, R., Tôrres, N. M., Furtado, M. M., and Marinho-Filho, J. (2010). Density of the near threatened jaguar panthera onca in the caatinga of north-eastern brazil. *Oryx*, 44(01):104–109.

Silveira, L., Jácomo, A. T., and Malzoni Furtado, M. (2005). Pampas cat ecology and conservation in the brazilian grasslands. *Cat Project of the Month, September*.

Simcharoen, S., Barlow, A. C., Simcharoen, A., and Smith, J. L. (2008). Home range size and daytime habitat selection of leopards in huai kha khaeng wildlife sanctuary, thailand. *Biological Conservation*, 141(9):2242–2250.

Skinner, J. D. and Chimimba, C. T. (2005). *The mammals of the southern African sub-region*. Cambridge University Press.

Sollmann, R., Furtado, M. M., Gardner, B., Hofer, H., Jácomo, A. T., Tôrres, N. M., and Silveira, L. (2011). Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central brazil. *Biological Conservation*, 144(3):1017–1024.

Sollmann, R., Furtado, M. M., Hofer, H., Jácomo, A. T., Tôrres, N. M., and Silveira, L. (2012a). Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central brazil. *Mammalian Biology-Zeitschrift für Säugetierkunde*, 77(1):41–46.

Sollmann, R., Gardner, B., and Belant, J. L. (2012b). How does spatial study design influence density estimates from spatial capture-recapture models. *PloS one*, 7(4):e34575.

Sollmann, R., Gardner, B., Chandler, R. B., Shindle, D. B., Onorato, D. P., Royle, J. A., and O'Connell, A. F. (2013a). Using multiple data sources provides density estimates for endangered Florida panther. *Journal of Applied Ecology*, 50(4):961–968.

Sollmann, R., Gardner, B., Parsons, A. W., Stocking, J. J., McClintock, B. T., Simons, T. R., Pollock, K. H., and O'Connell, A. F. (2013b). A spatial mark-resight model augmented with telemetry data. *Ecology*, 94(3):553–559.

Stache, A., Löttker, P., and Heurich, M. (2012). Red deer telemetry: dependency of the position acquisition rate and accuracy of gps collars on the structure of a temperate forest dominated by european beech. *Silva Gabreta*, 18(1):35–48.

Stein, A. B., Fuller, T. K., DeStefano, S., and Marker, L. L. (2011). Leopard population and home range estimates in north-central namibia. *African Journal of Ecology*, 49(3):383–387.

Sunquist, M. and Sunquist, F. (2002). *Wild cats of the world*. University of Chicago Press.

Suryawanshi, K. R., Bhatnagar, Y. V., Redpath, S., and Mishra, C. (2013). People, predators and perceptions: patterns of livestock depredation by snow leopards and wolves. *Journal of Applied Ecology*, 50(3):550–560.

Tambako, T. J. (2014). *Comfortable snow leopard cub*.

Theile, S. (2003). Fading footsteps: the killing and trade of snow leopards. Technical report, TRAFFIC International.

Thomas, L. and Marques, T. A. (2012). Passive acoustic monitoring for estimating animal density. *Acoustics Today*, 8(3):35–44.

Tobler, M., Carrillo-Percastegui, S., Leite Pitman, R., Mares, R., and Powell, G. (2008). An evaluation of camera traps for inventorying large-and medium-sized terrestrial rainforest mammals. *Animal Conservation*, 11(3):169–178.

Tobler, M. W. and Powell, G. V. (2013). Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. *Biological conservation*, 159:109–118.

Tomkiewicz, S. M., Fuller, M. R., Kie, J. G., and Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550):2163–2176.

Trolle, M., Noss, A. J., Lima, E. D. S., and Dalponte, J. C. (2007). Camera-trap studies of maned wolf density in the Cerrado and the Pantanal of Brazil. *Biodiversity and Conservation*, 16(4):1197–1204.

Ullas Karanth, K. (1988). Analysis of predator-prey balance in bandipur tiger reserve with reference to census reports. *Journal of the Bombay Natural History Society*, 85(1):1–8.

Van Niel, T. G., McVicar, T. R., and Datt, B. (2005). On the relationship between training sample size and data dimensionality: Monte carlo analysis of broadband multi-temporal classification. *Remote Sensing of Environment*, 98(4):468–480.

VIBBER, B. (2016). *Snow leopard range*.

Vitousek, P. M., Mooney, H. A., Lubchenco, J., and Melillo, J. M. (1997). Human domination of earth's ecosystems. *Science*, 277(5325):494–499.

Walters, C. L., Collen, A., Lucas, T., Mroz, K., Sayer, C. A., and Jones, K. E. (2013). Challenges of using bioacoustics to globally monitor bats. In Adams, R. A. and Pedersen, S. C., editors, *Bat Evolution, Ecology, and Conservation*, pages 479–499. Springer.

Walters, C. L., Freeman, R., Collen, A., Dietz, C., Brock Fenton, M., Jones, G., Obrist, M. K., Puechmaille, S. J., Sattler, T., Siemers, B. M., et al. (2012). A continental-scale tool for acoustic identification of European bats. *Journal of Applied Ecology*, 49(5):1064–1074.

Wang, S. W. and Macdonald, D. W. (2009). The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of bhutan. *Biological Conservation*, 142(3):606–613.

Wegge, P., Pokheral, C. P., and Jnawali, S. R. (2004). Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. *Animal Conservation*, 7(03):251–256.

Weingarth, K., Zeppenfeld, T., Heibl, C., Heurich, M., Bufka, L., Daniszová, K., and Müller, J. (2015). Hide and seek: extended camera-trap session lengths and autumn provide best parameters for estimating lynx densities in mountainous areas. *Biodiversity and Conservation*, 24(12):2935–2952.

White, G. C. (1982). *Capture-recapture and removal methods for sampling closed populations*. Los Alamos National Laboratory.

Wibisono, H. T., Figel, J. J., Arif, S. M., Ario, A., and Lubis, A. H. (2009). Assessing the sumatran tiger panthera tigris sumatrae population in batang gadis national park, a new protected area in indonesia. *Oryx*, 43(04):634–638.

Wilman, E. A. and Wilman, E. N. (2015). Modeling outcomes of approaches to sustained human and snow leopard coexistence. *Conservation Biology*.

Wilson, K. R. and Anderson, D. R. (1985). Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy*, 66(1):13–21.

Wilting, A., Mohamed, A., Ambu, L. N., Lagan, P., Mannan, S., Hofer, H., and Sollmann, R. (2012). Density of the vulnerable sunda clouded leopard neofelis diardi in two commercial forest reserves in sabah, malaysian borneo. *Oryx*, 46(03):423–426.

Wright, S. J. and Hubbell, S. P. (1983). Stochastic extinction and reserve size: a focal species approach. *Oikos*, pages 466–476.

Yapp, W. (1956). The theory of line transects. *Bird Study*, 3(2):93–104.

Yoccoz, N. G., Nichols, J. D., and Boulinier, T. (2001). Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution*, 16(8):446–453.

Yoshizaki, J., Pollock, K. H., Brownie, C., and Webster, R. A. (2009). Modeling misidentification errors in capture-recapture studies using photographic identification of evolving marks. *Ecology*, 90(1):3–9.

Zero, V. H., Sundaresan, S. R., O'Brien, T. G., and Kinnaird, M. F. (2013). Monitoring an endangered savannah ungulate, Grevy's zebra (*Equus grevyi*): choosing a method for estimating population densities. *Oryx*, 47(03):410–419.

Zimmermann, F., Breitenmoser-Würsten, C., Molinari-Jobin, A., and Breitenmoser, U. (2012). Optimizing the size of the area surveyed for monitoring a eurasian lynx (lynx lynx) population in the swiss alps by means of photographic capture-recapture. integrative zoology 8: 232-243. *Integrative Zoology*, 8:232–243.

Appendix A

Chapter 1

Terms for felids	Terms for camera trapping
Panthera OR Pantherinae OR Feline OR Felid OR Felidae OR Felinae OR Big cat OR Cat OR Lion OR Jaguar OR Leopard OR Tiger OR Ocelot OR cougar OR Snow leopard OR Sunda clouded leopard OR Cheetah OR Lynx OR Puma OR Panthera Leo OR Panthera onca OR Panthera pardus OR Panthera tigris OR Uncia uncia OR Neofelis nebulosa OR Neofelis diardi	Camera traps OR trapping cameras OR photograph* Capture OR CMR OR Capture-mark-recapture OR Capture-recapture OR Spatially Explicit Capture- recapture

Table A.1: Table of search terms use in Web of Science

A.1 Papers reviewed

Andean cat: (Reppucci et al., 2011); Cheetah: (Marnewick et al., 2008); European Wildcat: (Anile et al., 2010), Geoffroys cat: (Caruso et al., 2012; Pereira et al., 2006); Iberian Lynx: (Garrote et al., 2011, 2012; López-Parra et al., 2012); Jaguar: (de la Torre and Medellín, 2011; Negroes et al., 2012; Noss et al., 2012; Núñez-Pérez, 2011; Paviolo et al., 2008; Silveira et al., 2010; Sollmann et al., 2012a, 2011); Leopard: (Balme et al., 2009; Ghoddousi et al., 2008; Gray and Prum, 2012; Harihar et al., 2009a, 2011; Kalle et al., 2011; Ramesh et al., 2012; Stein et al., 2011; Wang and Macdonald, 2009); Ocelot: (Di Bitetti et al., 2008; Dillon and Kelly, 2008; Fusco-Costa et al., 2010; González-Maya and Cardenal-Porras, 2012; Kolowski and Alonso, 2010; Maffei and Noss, 2008; Noss et al., 2012; Negroes et al., 2012);

Pampas cat: (Caruso et al., 2012; Gardner et al., 2010a); Puma: (Kelly et al., 2008; Negrões et al., 2010; Negroes et al., 2012; Paviolo et al., 2009; Sollmann et al., 2012a); Snow Leopard: (Jackson et al., 2009; Janečka et al., 2011; McCarthy et al., 2008); Sunda Clouded Leopard: (Brodie and Giordano, 2012; Wilting et al., 2012); Tiger: (Gopalaswamy et al., 2012; Harihar et al., 2009b,c, 2011; Kalle et al., 2011; Lynam et al., 2009; Ramesh et al., 2012; Rayan and Mohamad, 2009; Royle et al., 2009a,b; Sharma et al., 2010; Wang and Macdonald, 2009; Wibisono et al., 2009)

A.2 Length and size of surveys

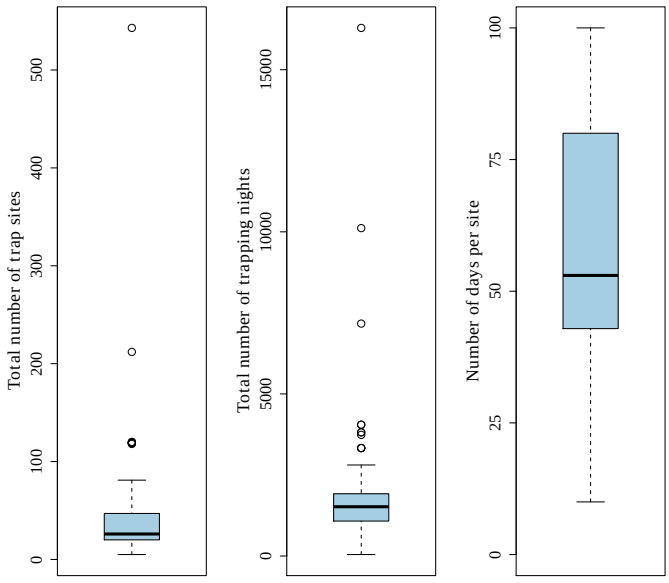


Figure A.1: The length of surveys completed shown in the number of camera site, average length of time per site and total survey effort. Where the box of each boxplot represents the middle 50% of the data and the sticks represent the upper and lower quartiles of the data up to 1.96 of the interquartile range, with data points outside this being classified as outliers.

Variable	Mean (sd)	Median (IQR)
Grid size (km^2)	174.0(297.1)	66.5 (49.0-107.0)
Intertrap distance	2.4 (3.3)	2 (1.2-2.9)
Number of cameras	43.0 (61.1)	26 (20-47)
Total trapping effort	1775.4 (1771.2)	1520.0 (1077.5 -1920.0)
Number days per site	54.9 (24.6)	53.0 (42.9-80.0)

Table A.2: Summary statistics of the survey setup. sd - standard deviation; IQR - the interquartile range

A.3 Home range estimates

European wildcat: (Monterroso et al., 2009); Geoffroys cat (Pereira et al., 2006); Iberian lynx (Gil-Sánchez et al., 2011); Jaguar (Núñez-Pérez, 2011; Scognamillo et al., 2003); Leopard (Simcharoen et al., 2008); Ocelot (Dillon and Kelly, 2008; Noss et al., 2012); Pampas cat:(Silveira et al., 2005); Puma (Scognamillo et al., 2003); Sunda clouded leopard: Not available; Tiger: (Karanth and Sunquist, 2000; Sharma et al., 2010)

Appendix B

Chapter 2

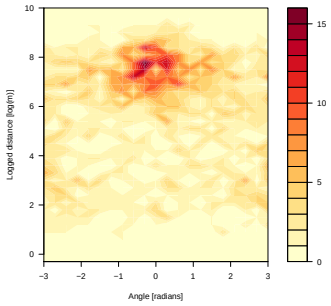
B.1 Equations for calculating varaibles

$$d = 2r\arcsin\left(\sqrt{\sin^2\left(\frac{\phi_2-\phi_1}{2}\right)+\cos(\phi_1)\cos(\phi_2)\sin^2\left(\frac{\lambda_2-\lambda_1}{2}\right)}\right) \quad \text{(B.1)}$$

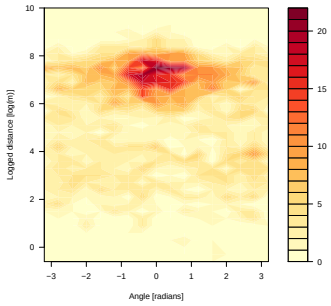
Where ϕ_1, ϕ_2 are the latitude of location 1 and 2 respectively; λ_1, λ_2 are the longitude of location 1 and 2 respectively; r is the radius of the earth; d is the great circle distance.

Table B.1: Variables that have been calculated with their formulae

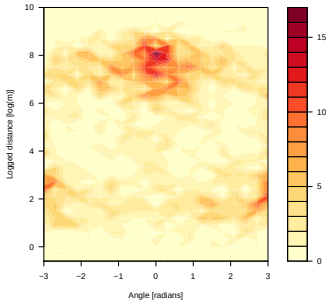
Variable Name	Unit	Description	Formula
Sex		The sex of the animal	Split.string(AnimID[i])[1]
Time_Difference	Seconds	The time since the last location	Date_Time[i] - Date_Time[i-1]
Dist_Difference	Meters	The displacement since the last location	Haversines formula, Equation (B.1)
Speed_mps	Meters/Second	The minimum speed required to reach current location from last	$\frac{Dist\_Difference[i]}{Time\_Difference[i]}$
Bearing	Radians	The angle of travel (from north), based last two locations	$\arctan(\frac{\delta(Latitude)}{\delta(Longitude)})$
ChangeAngle	Radians	The change in the bearing	Bearing[i] - Bearing[i-1]



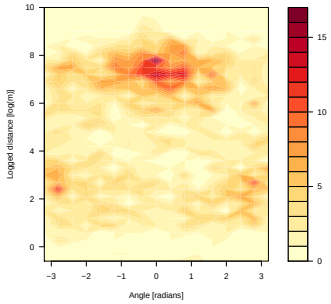
(a) A heatmap of displacement by turn angle for male summer subpopulation. Where red indicates a higher density and yellow indicates a lower density



(b) A heatmap of displacement by turn angle for female summer subpopulation. Where red indicates a higher density and yellow indicates a lower density



(a) A heatmap of displacement by turn angle for male winter subpopulation. Where red indicates a higher density and yellow indicates a lower density



(b) A heatmap of displacement by turn angle for female winter subpopulation. Where red indicates a higher density and yellow indicates a lower density

B.2 Displacement and turn angle

B.3 Data blocks

Block ID	Animal name	Sex	Year	Days (hours) surveyed over	Locations Locations	Useable 5hrs apart locations for model
S01	Zaraa	F	2010	76.7 (1840)	226	85
S02	Khashaa	F	2011	91.5 (2195)	407	216
S03	Khashaa	F	2012	91.5 (2195)	237	90
S04	Anu	F	2011	91.7 (2200)	342	195
S05	Anu	F	2012	91.7 (2200)	262	135
S06	Lasya	F	2011	91.7 (2200)	312	159
S07	Lasya	F	2012	91.7 (2200)	291	152
S08	Agnes	F	2012	91.7 (2200)	325	188
S09	Agnes	F	2013	90.8 (2180)	293	155
S10	Dagina	F	2012	88.5 (2125)	219	78
S11	Dagina	F	2013	91.2 (2190)	301	153
S12	Ariunbeleg	F	2013	91.8 (2204)	272	54
S13	Aztai	M	2010	91.2 (2190)	261	138
S14	Aztai	M	2011	91.7 (2200)	365	252
S15	Ariun	M	2012	91.7 (2200)	280	103
S16	Ariun	M	2013	91.5 (2195)	321	158
S17	Shonkhor	M	2011	91.7 (2200)	391	232
S18	Khavar	M	2010	91.5 (2195)	293	159
S19	Khavar	M	2011	91.5 (2195)	328	185
S20	Aylagch	M	2012	91.5 (2195)	277	123

Table B.2: Details of selected blocks of movement data during the summer season

Block ID	Animal name	Sex	Year	Days (hours) surveyed over	Locations Locations	Useable 5hrs apart locations for model
W01	Zaraa	F	2010 - 2011	91.3 (2190)	272	114
W02	Khashaa	F	2010 - 2011	91.7 (2200)	336	171
W03	Khashaa	F	2011 - 2012	91.2 (2190)	302	151
W04	Khashaa	F	2012 - 2013	91.7 (2200)	293	145
W05	Anu	F	2011 - 2012	91.9 (2205)	344	233
W06	Lasya	F	2011 - 2012	91.9 (2205)	346	223
W07	Agnes	F	2012 - 2013	91.2 (2190)	268	125
W08	Dagina	F	2012 - 2013	91.7 (2200)	323	188
W09	Ariunbeleg	F	2012 - 2013	91.2 (2189)	243	58
W10	Aztai	M	2010 - 2011	91.2 (2190)	297	203
W11	Ariun	M	2012 - 2013	91 (2185)	331	193
W12	Tsagaan	M	2010 - 2011	91.9 (2205)	336	206
W13	Shonkhor	M	2010 - 2011	87.1 (2090)	377	297
W14	Khavar	M	2011 - 2012	91.7 (2200)	347	228
W15	Aylagch	M	2011 - 2012	91.7 (2200)	280	149
W16	Aylagch	M	2012 - 2013	91.7 (2200)	297	173

Table B.3: Selected blocks of winter data

Test	p-value	Significance level
Summer female Vs Summer male	0.047	**
Summer female Vs Winter female	0.262	-
Summer male Vs Winter male	0.670	-
Winter female Vs Winter male	0.176	-

Table B.4: Tests for differences between activity measures when made up of 1km grids. Where: - is not significant, * is possibly significant, ** is significant and *** is highly significant; before correction for multiple testing

Test	p-value	Significance level
summer female: S01vsS02	0.010	**
summer female: S01vsS03	0.000	***
summer female: S01vsS04	0.009	**
summer female: S01vsS05	0.165	-
summer female: S01vsS06	0.007	**
summer female: S01vsS07	0.007	**
summer female: S01vsS08	0.346	-
summer female: S01vsS09	0.135	-
summer female: S01vsS10	0.698	-
summer female: S01vsS11	0.037	**
summer female: S01vsS12	0.515	-
summer female: S02vsS03	0.056	*
summer female: S02vsS04	0.415	-
summer female: S02vsS05	0.216	-
summer female: S02vsS06	0.074	*
summer female: S02vsS07	0.292	-
summer female: S02vsS08	0.062	*
summer female: S02vsS09	0.374	-
summer female: S02vsS10	0.121	-
summer female: S02vsS11	0.839	-
summer female: S02vsS12	0.047	**
summer female: S03vsS04	0.055	*
summer female: S03vsS05	0.001	***
summer female: S03vsS06	0.000	***
summer female: S03vsS07	0.070	*
summer female: S03vsS08	0.000	***
summer female: S03vsS09	0.007	**
summer female: S03vsS10	0.002	**
summer female: S03vsS11	0.021	**
summer female: S03vsS12	0.039	**
summer female: S04vsS05	0.132	-
summer female: S04vsS06	0.070	*
summer female: S04vsS07	0.947	-
summer female: S04vsS08	0.026	**

Table B.5: Tests for differences between displacement between individual females during the summer season
Where: - is not significant, * is possibly significant, ** is significant and *** is highly significant; before correction for multiple testing

Test	p-value	Significance level
summer female: S04vsS09	0.148	-
summer female: S04vsS10	0.029	**
summer female: S04vsS11	0.509	-
summer female: S04vsS12	0.003	**
summer female: S05vsS06	0.150	-
summer female: S05vsS07	0.088	*
summer female: S05vsS08	0.189	-
summer female: S05vsS09	0.639	-
summer female: S05vsS10	0.416	-
summer female: S05vsS11	0.251	-
summer female: S05vsS12	0.176	-
summer female: S06vsS07	0.034	**
summer female: S06vsS08	0.033	**
summer female: S06vsS09	0.067	*
summer female: S06vsS10	0.019	**
summer female: S06vsS11	0.101	-
summer female: S06vsS12	0.001	**
summer female: S07vsS08	0.020	**
summer female: S07vsS09	0.057	*
summer female: S07vsS10	0.021	**
summer female: S07vsS11	0.244	-
summer female: S07vsS12	0.006	**
summer female: S08vsS09	0.345	-
summer female: S08vsS10	0.666	-
summer female: S08vsS11	0.096	*
summer female: S08vsS12	0.233	-
summer female: S09vsS10	0.384	-
summer female: S09vsS11	0.648	-
summer female: S09vsS12	0.072	*
summer female: S10vsS11	0.114	-
summer female: S10vsS12	0.590	-
summer female: S11vsS12	0.034	**

Table B.6: Tests for differences between displacement between individual females during the summer season
Where: - is not significant, * is possibly significant, ** is significant and *** is highly significant; before correction for multiple testing

Test	p-value	Significance level
summer male: S13vsS14	0.584	-
summer male: S13vsS15	0.373	-
summer male: S13vsS16	0.000	***
summer male: S13vsS17	0.002	**
summer male: S13vsS18	0.484	-
summer male: S13vsS19	0.160	-
summer male: S13vsS20	0.301	-
summer male: S14vsS15	0.204	-
summer male: S14vsS16	0.000	***
summer male: S14vsS17	0.000	***
summer male: S14vsS18	0.303	-
summer male: S14vsS19	0.172	-
summer male: S14vsS20	0.026	**
summer male: S15vsS16	0.006	**
summer male: S15vsS17	0.003	**
summer male: S15vsS18	0.283	-
summer male: S15vsS19	0.241	-
summer male: S15vsS20	0.268	-
summer male: S16vsS17	0.000	***
summer male: S16vsS18	0.000	***
summer male: S16vsS19	0.006	**
summer male: S16vsS20	0.000	***
summer male: S17vsS18	0.073	*
summer male: S17vsS19	0.010	**
summer male: S17vsS20	0.005	**
summer male: S18vsS19	0.079	*
summer male: S18vsS20	0.252	-
summer male: S19vsS20	0.006	**

Table B.7: Tests for differences between displacement between individual males during the summer season
Where: - is not significant, * is possibly significant, ** is significant and *** is highly significant; before correction for multiple testing

Test	p-value	Significance level
winter female: W01vsW02	0.003	**
winter female: W01vsW03	0.393	-
winter female: W01vsW04	0.064	*
winter female: W01vsW05	0.000	***
winter female: W01vsW06	0.061	*
winter female: W01vsW07	0.028	**
winter female: W01vsW08	0.007	**
winter female: W01vsW09	0.014	**
winter female: W02vsW03	0.008	**
winter female: W02vsW04	0.101	-
winter female: W02vsW05	0.050	*
winter female: W02vsW06	0.001	***
winter female: W02vsW07	0.000	***
winter female: W02vsW08	0.026	**
winter female: W02vsW09	0.005	**
winter female: W03vsW04	0.248	-
winter female: W03vsW05	0.025	**
winter female: W03vsW06	0.691	-
winter female: W03vsW07	0.009	**
winter female: W03vsW08	0.144	-
winter female: W03vsW09	0.080	*
winter female: W04vsW05	0.084	*
winter female: W04vsW06	0.132	-
winter female: W04vsW07	0.001	***
winter female: W04vsW08	0.452	-
winter female: W04vsW09	0.035	**
winter female: W05vsW06	0.138	-
winter female: W05vsW07	0.005	**
winter female: W05vsW08	0.353	-
winter female: W05vsW09	0.298	-
winter female: W06vsW07	0.030	**
winter female: W06vsW08	0.422	-
winter female: W06vsW09	0.292	-
winter female: W07vsW08	0.004	**
winter female: W07vsW09	0.605	-
winter female: W08vsW09	0.139	-

Table B.8: Tests for differences between displacement between individual females during the winter season
Where: - is not significant, * is possibly significant, ** is significant and *** is highly significant; before correction for multiple testing

Test	p-value	Significance level
winter male: W10vsW11	0.003	**
winter male: W10vsW12	0.216	-
winter male: W10vsW13	0.104	-
winter male: W10vsW14	0.026	**
winter male: W10vsW15	0.629	-
winter male: W10vsW16	0.993	-
winter male: W11vsW12	0.381	-
winter male: W11vsW13	0.185	-
winter male: W11vsW14	0.006	**
winter male: W11vsW15	0.001	***
winter male: W11vsW16	0.023	**
winter male: W12vsW13	0.858	-
winter male: W12vsW14	0.022	**
winter male: W12vsW15	0.039	**
winter male: W12vsW16	0.271	-
winter male: W13vsW14	0.125	-
winter male: W13vsW15	0.045	**
winter male: W13vsW16	0.327	-
winter male: W14vsW15	0.032	**
winter male: W14vsW16	0.060	*
winter male: W15vsW16	0.676	-

Table B.9: Tests for differences between displacement between individual males during the winter season
Where: - is not significant, * is possibly significant, ** is significant and *** is highly significant; before correction for multiple testing

B.4 Parameters of random walk movement

	Male	Female
Logged displacement, mean (sd)	6.9 (2.07)	7.2 (2.17)
Turn angle, mean (sd)	0.0 (1.72)	0.0 (1.72)

Table B.10: Random walk parameters

B.5 Parameters of movement clusters

Cluster	Centre logged metre	Centre turn angle	Probability
1	3.97	0.30	0.24
2	4.63	2.72	0.10
3	7.32	-0.05	0.56
4	4.56	-2.64	0.11

Table B.11: The cluster number and the centre for each cluster for male clusters

1.539	0	0	1.360
1.830	0	0	0.303
0.879	0	0	1.181
1.925	0	0	0.350

Table B.12: The covariance matrix for the clusters for male clusters

0.304	0.176	0.304	0.216
0.238	0.175	0.375	0.213
0.185	0.037	0.722	0.057
0.308	0.244	0.308	0.141

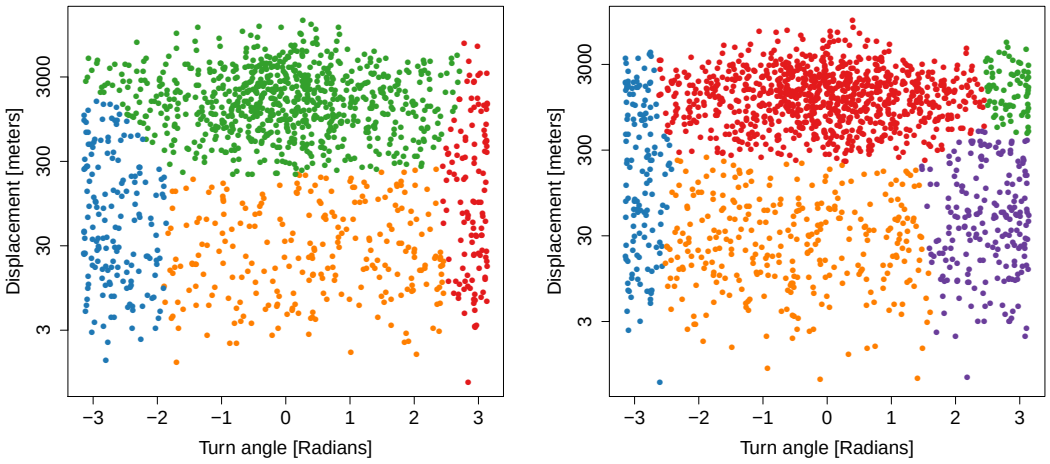
Table B.13: The markov matrix of transitions for male clusters

625,000,000

Table B.14: The average home range size in square meters for males in the training sample

Cluster	Centre logged metre	Centre turn angle	Probability
1	3.37	-1.08	0.18
2	4.78	2.93	0.07
3	4.91	-2.94	0.06
4	3.82	1.82	0.13
5	7.15	-0.07	0.56

Table B.15: The cluster number and the centre for each cluster for female clusters



(a) Alternative clustering for all male data using a mclust method in R (Fraley et al., 2012)

(b) Alternative clustering for all male data using a mclust method in R (Fraley et al., 2012)

1.403	0	0.002	1.029
1.953	0	0.004	0.154
1.956	0	0.004	0.157
1.644	0	0.003	0.663
0.704	0	-0.004	1.312

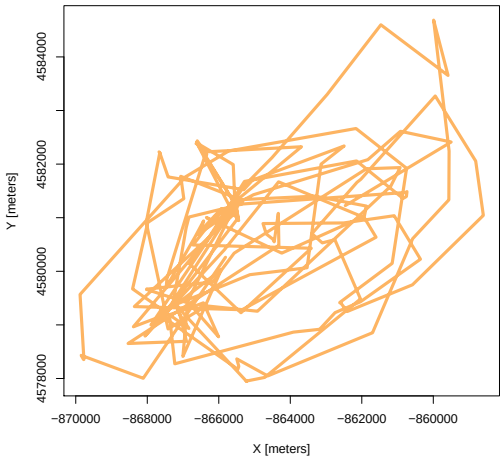
Table B.16: The covariance matrix for the clusters for female clusters

0.231	0.147	0.161	0.231	0.231
0.290	0.116	0.101	0.174	0.319
0.373	0.090	0.075	0.149	0.313
0.271	0.140	0.122	0.196	0.271
0.105	0.055	0.039	0.080	0.721

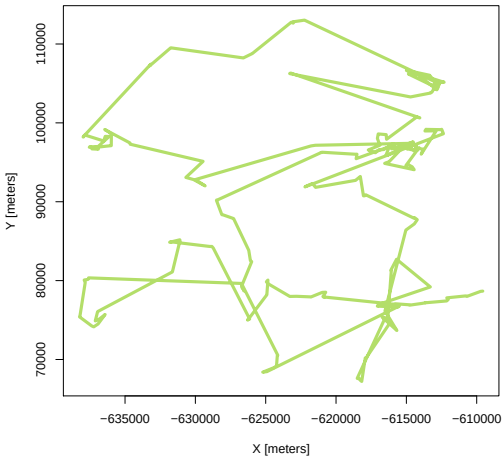
Table B.17: The markov matrix of transitions for female clusters

430,000,000

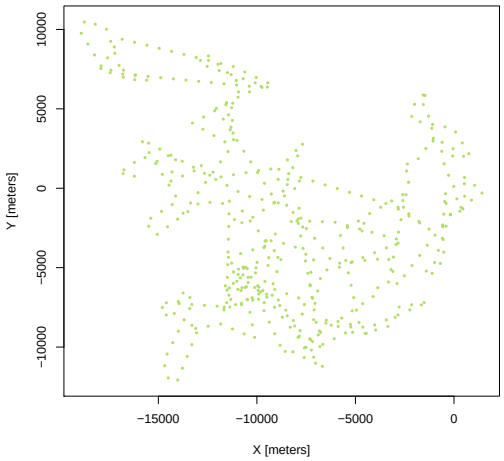
Table B.18: The average home range size in square meters for females in the training sample



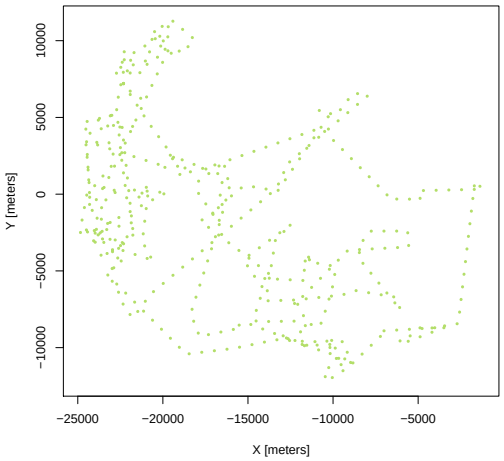
(a) Example of female movement path from the validation dataset



(b) Example of female movement path created by random walk

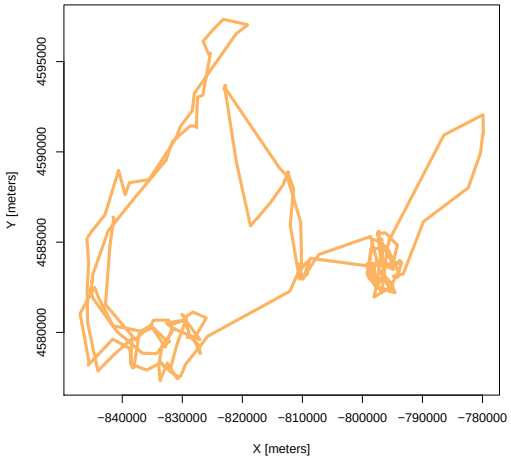


(c) Example of female movement path created by clustered movement with no transition

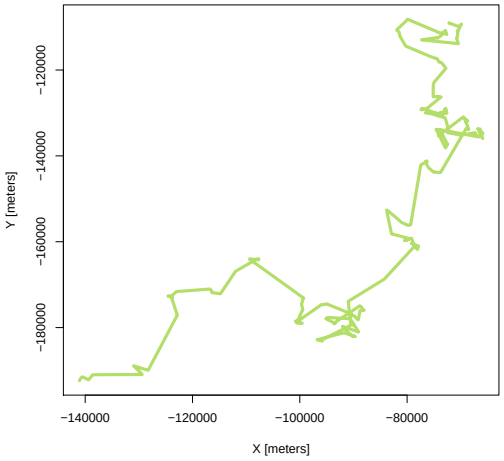


(d) Example of female movement path created by clustered movement with Markov transition

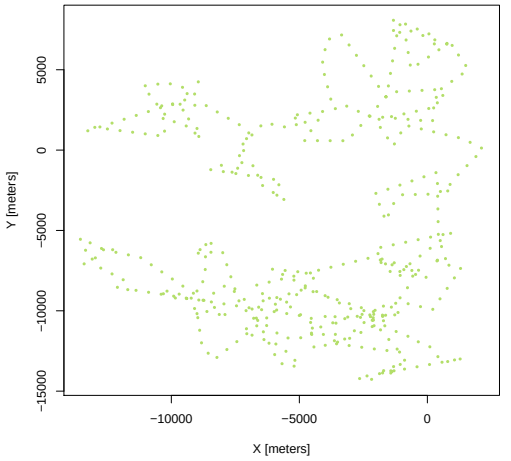
B.6 Example movement



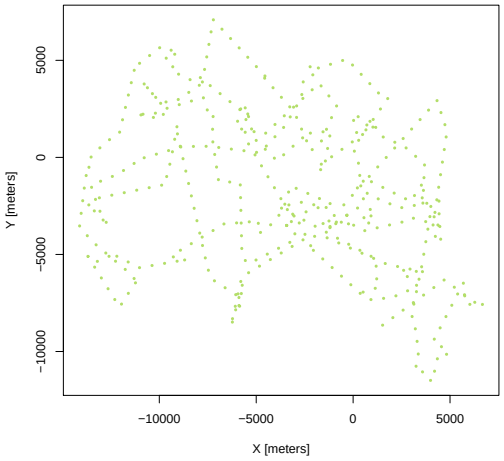
(a) Example of male movement path from the validation dataset



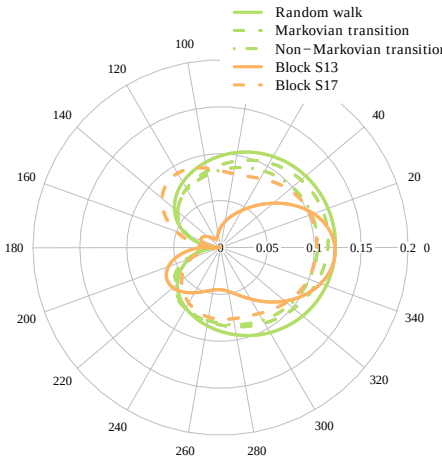
(b) Example of male movement path created by random walk



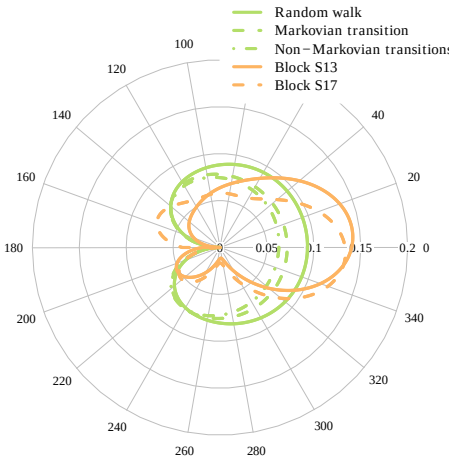
(c) Example of male movement path created by clustered movement with no transition



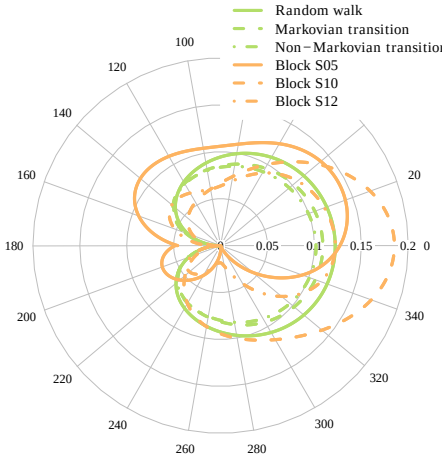
(d) Example of male movement path created by clustered movement with Markov transition



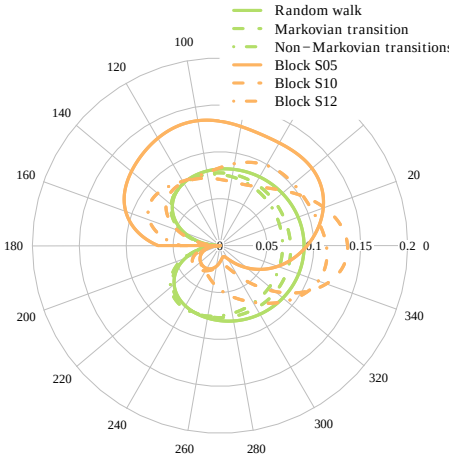
(a) Turn angle after 10 hours



(b) Turn angle after 25 hours



(c) Turn angle after 10 hours



(d) Turn angle after 25 hours

Figure B.6: The distribution of distance and turn angle for females

B.7 Validation Plots

Appendix C

Chapter 3

Capture rate	Capture Probability (5day)	Density estimates	Reference
0.09	NA	NA	(McCarthy et al., 2010)
0.66	NA	NA	(McCarthy et al., 2010)
0.085	NA	0.15	(McCarthy et al., 2008)
0.557	NA	0.87	(McCarthy et al., 2008)
1.102	NA	0.74	(McCarthy et al., 2008)
10.77	0.432	0.72-1.52	(Jackson et al., 2009)
0.257	NA	NA	(Sathyakumar et al., 2011)
0.840	0.346	8.49	(Jackson et al., 2006)
0.495	0.333	4.45	(Jackson et al., 2006)

Table C.1: The capture rate for snow leopards from multiple sources. Where capture rate is the number of captures per 100 days

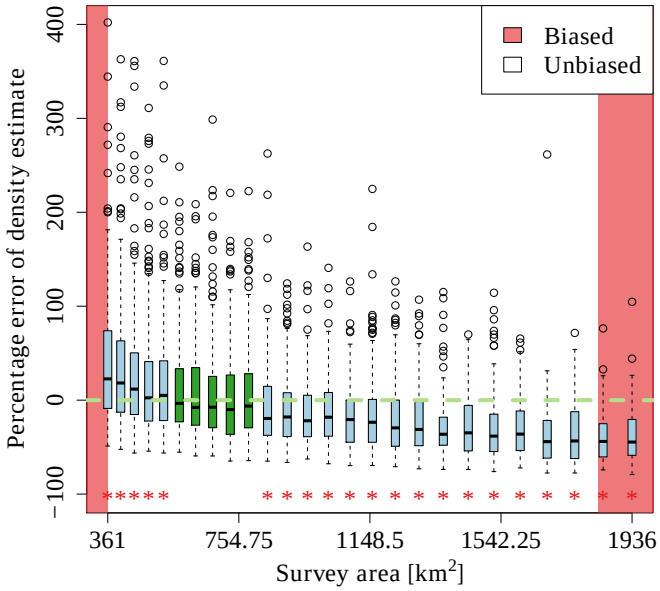
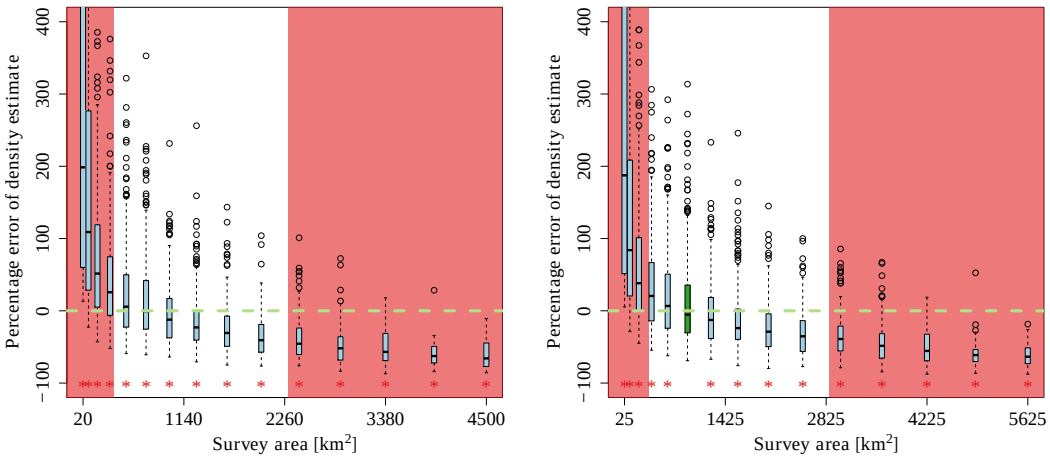
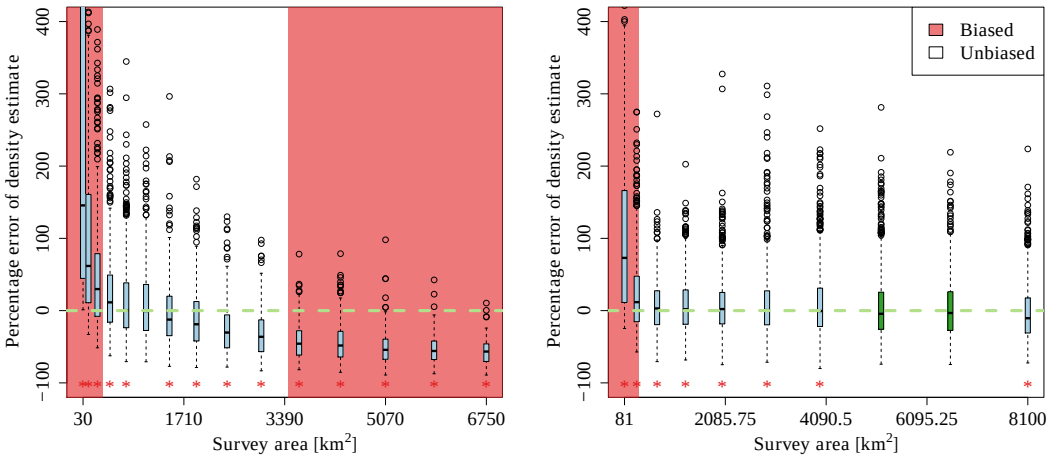


Figure C.1: The percentage error of densities estimated using SECR, when 26 cameras were used, with inter trap distances ranging from 1 km to 15 km. The average home range size for each animal was kept as constant between each set of simulations, 360 km. Where based on the guidelines discussed in chapter 2, box plots in the red area are biased due to small survey areas or wide inter trap distances. Green box plots with a red star below indicates that the medium bias is significantly different from 0.



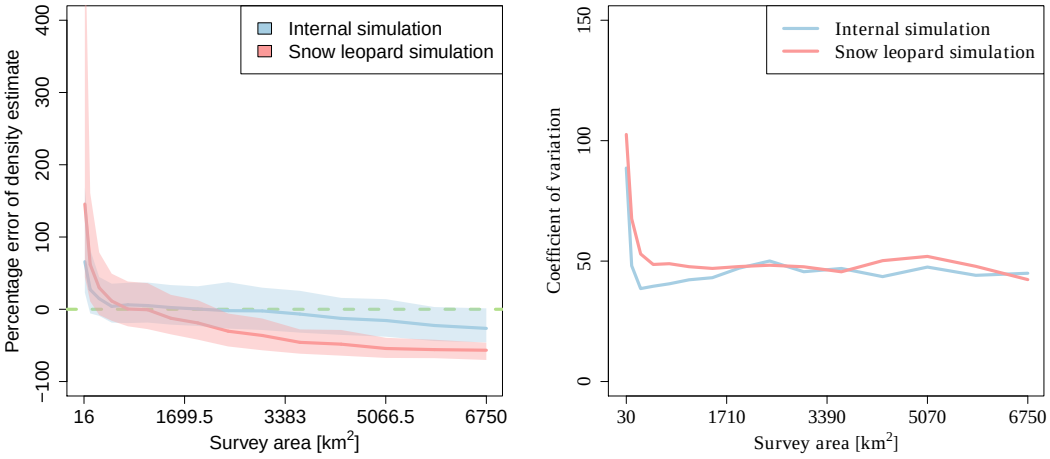
(a) 30 cameras **(b)** 36 cameras

Figure C.2: The percentage error of densities estimated using SECR, when a) 30 cameras and b)36 cameras were used, with inter-trap distances ranging from 1 km to 15 km and 1 km to 10 km respectively. The average home range size for each animal was kept as constant between each set of simulations, 360 km. Where based on the guidelines discussed in chapter 2, box plots in the red area are biased due to small survey areas, and box plots shaded in dark blue are biased due to wide inter trap distances. Red stars indicate that the median of the above box is significantly different from 0 percentage error.



(a) 42 cameras **(b)** 100 cameras

Figure C.3: The percentage error of densities estimated using SECR, when a) 42 cameras and b)100 cameras were used, with inter-trap distances ranging from 1 km to 15 km and 1 km to 10 km respectively. The average home range size for each animal was kept as constant between each set of simulations, 360 km. Where based on the guidelines discussed in chapter 2, box plots in the red area are biased due to small survey areas, and box plots shaded in dark blue are biased due to wide inter trap distances. Red stars indicate that the median of the above box is significantly different from 0 percentage error.



(a) Accuracy **(b)** Precision

Figure C.4: The a) accuracy and b) precision of the SECR density estimate when 42 were used, with inter-trap distances ranging from 1 km to 15 km and 1 km to 10 km respectively. The average home range size for each animal was kept as constant between each set of simulations, 360 km. Where light blue, and pink represent the capture matrices calculated through the internal simulation and the snow leopard simulation represectively.

Area (Spacing) 26cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
16km^2 (1km)	0.33 (0)	-0.12 (0.25)	-0.11 (0.27)
64km^2 (2km)	-0.03 (0.67)	0.3 (0)	-0.28 (0)
144km^2 (3km)	0.03 (0.66)	0.18 (0)	-0.16 (0.01)
256km^2 (4km)	0.14 (0.02)	0 (0.95)	0.11 (0.08)
400km^2 (5km)	-0.01 (0.83)	0.03 (0.6)	0.31 (0)
576km^2 (6km)	-0.04 (0.54)	-0.02 (0.79)	0.5 (0)
784km^2 (7km)	0.06 (0.37)	-0.2 (0)	0.61 (0)
1024km^2 (8km)	-0.14 (0.06)	0.06 (0.38)	0.6 (0)
1296km^2 (9km)	-0.1 (0.21)	-0.06 (0.45)	0.71 (0)
1600km^2 (10km)	-0.22 (0.03)	0.01 (0.96)	0.76 (0)
1936km^2 (11km)	-0.49 (0)	0.25 (0.02)	0.83 (0)
2304km^2 (12km)	-0.27 (0.01)	-0.03 (0.77)	0.8 (0)
2704km^2 (13km)	-0.38 (0)	-0.08 (0.56)	0.88 (0)
3136km^2 (14km)	-0.17 (0.22)	-0.46 (0)	0.87 (0)
3600km^2 (15km)	-0.58 (0)	0.02 (0.91)	0.87 (0)

Table C.2: Correlation between the number of captures and the estimated value g_0, σ, and density, for different levels of survey areas when 25 cameras are used

Area (Spacing) 43cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
30km^2 (1km)	0.26 (0)	0.11 (0.11)	-0.17 (0.01)
120km^2 (2km)	0.04 (0.37)	0.28 (0)	-0.16 (0)
270km^2 (3km)	0.07 (0.11)	0.17 (0)	0.05 (0.26)
480km^2 (4km)	0 (0.99)	0.16 (0)	0.26 (0)
750km^2 (5km)	-0.01 (0.74)	0.08 (0.06)	0.4 (0)
1080km^2 (6km)	-0.15 (0)	0.1 (0.01)	0.55 (0)
1470km^2 (7km)	-0.1 (0.03)	0.03 (0.5)	0.61 (0)
1920km^2 (8km)	-0.18 (0)	0.07 (0.14)	0.66 (0)
2430km^2 (9km)	-0.18 (0)	0.02 (0.67)	0.69 (0)
3000km^2 (10km)	-0.24 (0)	0.05 (0.39)	0.73 (0)
3630km^2 (11km)	-0.21 (0)	-0.01 (0.88)	0.75 (0)
4320km^2 (12km)	-0.31 (0)	0.02 (0.82)	0.75 (0)
5070km^2 (13km)	-0.16 (0.06)	-0.1 (0.21)	0.74 (0)
5880km^2 (14km)	-0.28 (0)	-0.1 (0.31)	0.78 (0)
6750km^2 (15km)	-0.36 (0)	-0.06 (0.52)	0.79 (0)

Table C.3: Correlation between the number of captures and the estimated value g_0, σ, and density, for different levels of survey areas when 42 cameras are used

Area (Spacing) 26cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
16km^2 (1km)	0.4 (0)	-0.12 (0.23)	-0.22 (0.02)
64km^2 (2km)	0.07 (0.38)	0.35 (0)	-0.53 (0)
144km^2 (3km)	0.13 (0.03)	0.22 (0)	-0.53 (0)
256km^2 (4km)	0.09 (0.13)	0.16 (0.01)	-0.5 (0)
400km^2 (5km)	-0.06 (0.35)	0.31 (0)	-0.58 (0)
576km^2 (6km)	-0.05 (0.39)	0.36 (0)	-0.63 (0)
784km^2 (7km)	-0.02 (0.76)	0.33 (0)	-0.62 (0)
1024km^2 (8km)	-0.1 (0.18)	0.38 (0)	-0.54 (0)
1296km^2 (9km)	-0.09 (0.27)	0.38 (0)	-0.52 (0)
1600km^2 (10km)	-0.2 (0.04)	0.56 (0)	-0.63 (0)
1936km^2 (11km)	-0.15 (0.16)	0.48 (0)	-0.55 (0)
2304km^2 (12km)	-0.15 (0.19)	0.56 (0)	-0.57 (0)
2704km^2 (13km)	-0.01 (0.97)	0.55 (0)	-0.72 (0)
3136km^2 (14km)	-0.11 (0.43)	0.61 (0)	-0.73 (0)
3600km^2 (15km)	0.33 (0.04)	0.28 (0.08)	-0.73 (0)

Table C.4: Correlation between the mean number of cameras an animal is captured and the estimated value g_0, σ, and density, for different levels of survey areas when 25 cameras are used

Area (Spacing) 43cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
30km^2 (1km)	0.32 (0)	0.13 (0.06)	-0.33 (0)
120km^2 (2km)	0.09 (0.07)	0.37 (0)	-0.55 (0)
270km^2 (3km)	0.12 (0)	0.32 (0)	-0.57 (0)
480km^2 (4km)	0.2 (0)	0.25 (0)	-0.59 (0)
750km^2 (5km)	0.18 (0)	0.22 (0)	-0.52 (0)
1080km^2 (6km)	0.1 (0.02)	0.26 (0)	-0.55 (0)
1470km^2 (7km)	0.01 (0.9)	0.32 (0)	-0.54 (0)
1920km^2 (8km)	-0.06 (0.23)	0.42 (0)	-0.59 (0)
2430km^2 (9km)	-0.02 (0.77)	0.41 (0)	-0.6 (0)
3000km^2 (10km)	-0.11 (0.04)	0.52 (0)	-0.58 (0)
3630km^2 (11km)	-0.03 (0.65)	0.39 (0)	-0.52 (0)
4320km^2 (12km)	0 (0.97)	0.54 (0)	-0.63 (0)
5070km^2 (13km)	-0.02 (0.81)	0.56 (0)	-0.61 (0)
5880km^2 (14km)	0.04 (0.66)	0.57 (0)	-0.67 (0)
6750km^2 (15km)	0.03 (0.74)	0.54 (0)	-0.58 (0)

Table C.5: Correlation between the mean number of cameras an animal is captured and the estimated value g_0, σ, and density, for different levels of survey areas when 42 cameras are used

Area (Spacing) 26cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
16km^2 (1km)	0.43 (0)	-0.17 (0.09)	-0.08 (0.4)
64km^2 (2km)	0.11 (0.18)	0.26 (0)	-0.36 (0)
144km^2 (3km)	0.04 (0.53)	0.2 (0)	-0.37 (0)
256km^2 (4km)	0.07 (0.26)	0.11 (0.08)	-0.27 (0)
400km^2 (5km)	-0.1 (0.11)	0.25 (0)	-0.26 (0)
576km^2 (6km)	-0.03 (0.59)	0.23 (0)	-0.31 (0)
784km^2 (7km)	-0.11 (0.1)	0.2 (0)	-0.11 (0.11)
1024km^2 (8km)	-0.11 (0.13)	0.24 (0)	-0.12 (0.1)
1296km^2 (9km)	-0.15 (0.06)	0.23 (0)	-0.05 (0.56)
1600km^2 (10km)	-0.11 (0.25)	0.25 (0.01)	-0.1 (0.32)
1936km^2 (11km)	-0.02 (0.88)	0.14 (0.19)	-0.23 (0.03)
2304km^2 (12km)	-0.3 (0.01)	0.31 (0)	0.03 (0.82)
2704km^2 (13km)	-0.07 (0.63)	0.25 (0.06)	-0.26 (0.06)
3136km^2 (14km)	-0.15 (0.3)	0.25 (0.08)	-0.22 (0.12)
3600km^2 (15km)	NA (NA)	NA (NA)	NA (NA)

Table C.6: Correlation between the maximum number of cameras an animal is captured and the estimated value g_0, σ, and density, for different levels of survey areas when 25 cameras are used

Area (Spacing) 43cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
30km^2 (1km)	0.4 (0)	-0.05 (0.49)	-0.1 (0.14)
120km^2 (2km)	0.15 (0)	0.21 (0)	-0.31 (0)
270km^2 (3km)	0.07 (0.09)	0.26 (0)	-0.32 (0)
480km^2 (4km)	0.08 (0.05)	0.22 (0)	-0.28 (0)
750km^2 (5km)	0.1 (0.01)	0.1 (0.01)	-0.14 (0)
1080km^2 (6km)	-0.01 (0.74)	0.18 (0)	-0.18 (0)
1470km^2 (7km)	0.01 (0.89)	0.16 (0)	-0.14 (0)
1920km^2 (8km)	-0.08 (0.09)	0.28 (0)	-0.2 (0)
2430km^2 (9km)	-0.09 (0.07)	0.26 (0)	-0.16 (0)
3000km^2 (10km)	-0.02 (0.77)	0.14 (0.01)	-0.06 (0.31)
3630km^2 (11km)	-0.14 (0.03)	0.21 (0)	-0.02 (0.79)
4320km^2 (12km)	-0.07 (0.36)	0.17 (0.02)	-0.13 (0.07)
5070km^2 (13km)	-0.16 (0.05)	0.24 (0)	0.04 (0.6)
5880km^2 (14km)	-0.01 (0.94)	0.14 (0.14)	-0.06 (0.55)
6750km^2 (15km)	-0.02 (0.85)	0.19 (0.05)	-0.18 (0.06)

Table C.7: Correlation between the maximum number of cameras an animal is captured and the estimated value g_0, σ, and density, for different levels of survey areas when 42 cameras are used

Area (Spacing) 26cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
16km^2 (1km)	0.42 (0)	-0.17 (0.08)	-0.17 (0.1)
64km^2 (2km)	0.11 (0.16)	0.32 (0)	-0.51 (0)
144km^2 (3km)	0.22 (0)	0.13 (0.03)	-0.48 (0)
256km^2 (4km)	0.24 (0)	0.03 (0.57)	-0.41 (0)
400km^2 (5km)	0.14 (0.03)	0.15 (0.01)	-0.55 (0)
576km^2 (6km)	0.17 (0.01)	0.13 (0.05)	-0.47 (0)
784km^2 (7km)	0.34 (0)	-0.02 (0.76)	-0.49 (0)
1024km^2 (8km)	0.41 (0)	-0.11 (0.12)	-0.58 (0)
1296km^2 (9km)	0.42 (0)	-0.15 (0.05)	-0.57 (0)
1600km^2 (10km)	0.39 (0)	0.01 (0.92)	-0.65 (0)
1936km^2 (11km)	0.21 (0.05)	0.11 (0.3)	-0.56 (0)
2304km^2 (12km)	0.45 (0)	-0.05 (0.66)	-0.7 (0)
2704km^2 (13km)	0.37 (0.01)	0.1 (0.48)	-0.74 (0)
3136km^2 (14km)	0.43 (0)	-0.05 (0.74)	-0.67 (0)
3600km^2 (15km)	0.64 (0)	-0.19 (0.25)	-0.71 (0)

Table C.8: Correlation between the percentage of recaptures and the estimated value g_0, σ, and density, for different levels of survey areas when 25 cameras are used

Area (Spacing) 43cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
30km^2 (1km)	0.34 (0)	0.1 (0.13)	-0.3 (0)
120km^2 (2km)	0.14 (0)	0.31 (0)	-0.5 (0)
270km^2 (3km)	0.21 (0)	0.23 (0)	-0.53 (0)
480km^2 (4km)	0.28 (0)	0.18 (0)	-0.57 (0)
750km^2 (5km)	0.28 (0)	0.16 (0)	-0.54 (0)
1080km^2 (6km)	0.35 (0)	0.04 (0.33)	-0.6 (0)
1470km^2 (7km)	0.28 (0)	0.04 (0.41)	-0.53 (0)
1920km^2 (8km)	0.31 (0)	0.05 (0.25)	-0.58 (0)
2430km^2 (9km)	0.32 (0)	0.08 (0.13)	-0.63 (0)
3000km^2 (10km)	0.37 (0)	0.03 (0.65)	-0.59 (0)
3630km^2 (11km)	0.48 (0)	-0.14 (0.04)	-0.6 (0)
4320km^2 (12km)	0.48 (0)	-0.02 (0.75)	-0.66 (0)
5070km^2 (13km)	0.43 (0)	0.08 (0.31)	-0.58 (0)
5880km^2 (14km)	0.5 (0)	0 (0.98)	-0.63 (0)
6750km^2 (15km)	0.52 (0)	-0.11 (0.26)	-0.63 (0)

Table C.9: Correlation between the percentage of recaptures and the estimated value g_0, σ, and density, for different levels of survey areas when 42 cameras are used

Area (Spacing) 26cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
16km^2 (1km)	-0.21 (0.03)	0.11 (0.26)	0.13 (0.18)
64km^2 (2km)	-0.18 (0.02)	-0.02 (0.79)	0.32 (0)
144km^2 (3km)	-0.24 (0)	0.11 (0.07)	0.33 (0)
256km^2 (4km)	-0.04 (0.53)	-0.03 (0.62)	0.53 (0)
400km^2 (5km)	-0.11 (0.07)	-0.06 (0.3)	0.71 (0)
576km^2 (6km)	-0.1 (0.12)	-0.14 (0.03)	0.81 (0)
784km^2 (7km)	-0.12 (0.07)	-0.19 (0.01)	0.85 (0)
1024km^2 (8km)	-0.34 (0)	0.13 (0.08)	0.86 (0)
1296km^2 (9km)	-0.31 (0)	0.03 (0.72)	0.91 (0)
1600km^2 (10km)	-0.35 (0)	0.02 (0.86)	0.91 (0)
1936km^2 (11km)	-0.52 (0)	0.19 (0.07)	0.94 (0)
2304km^2 (12km)	-0.42 (0)	0.01 (0.94)	0.95 (0)
2704km^2 (13km)	-0.47 (0)	-0.07 (0.61)	0.97 (0)
3136km^2 (14km)	-0.27 (0.06)	-0.4 (0)	0.95 (0)
3600km^2 (15km)	-0.7 (0)	0.1 (0.54)	0.95 (0)

Table C.10: Correlation between the percentage of animals and the estimated value g_0, σ, and density, for different levels of survey areas when 25 cameras are used

Area (Spacing) 43cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
30km^2 (1km)	-0.03 (0.64)	0.01 (0.86)	0.2 (0)
120km^2 (2km)	-0.08 (0.11)	0.02 (0.62)	0.36 (0)
270km^2 (3km)	-0.1 (0.01)	0.01 (0.81)	0.54 (0)
480km^2 (4km)	-0.21 (0)	0.06 (0.12)	0.72 (0)
750km^2 (5km)	-0.19 (0)	-0.01 (0.76)	0.77 (0)
1080km^2 (6km)	-0.32 (0)	0.08 (0.06)	0.83 (0)
1470km^2 (7km)	-0.21 (0)	0.02 (0.67)	0.83 (0)
1920km^2 (8km)	-0.28 (0)	0.03 (0.54)	0.85 (0)
2430km^2 (9km)	-0.28 (0)	-0.01 (0.81)	0.87 (0)
3000km^2 (10km)	-0.35 (0)	0.04 (0.49)	0.89 (0)
3630km^2 (11km)	-0.37 (0)	0.05 (0.48)	0.9 (0)
4320km^2 (12km)	-0.44 (0)	0.02 (0.81)	0.9 (0)
5070km^2 (13km)	-0.26 (0)	-0.14 (0.09)	0.89 (0)
5880km^2 (14km)	-0.41 (0)	-0.09 (0.32)	0.92 (0)
6750km^2 (15km)	-0.49 (0)	-0.01 (0.92)	0.92 (0)

Table C.11: Correlation between the percentage of animals and the estimated value g_0, σ, and density, for different levels of survey areas when 42 cameras are used

Area (Spacing) 26cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
16km^2 (1km)	0.09 (0.35)	0.21 (0.04)	-0.44 (0)
64km^2 (2km)	-0.21 (0.01)	0.6 (0)	-0.74 (0)
144km^2 (3km)	-0.24 (0)	0.57 (0)	-0.72 (0)
256km^2 (4km)	-0.37 (0)	0.62 (0)	-0.74 (0)
400km^2 (5km)	-0.4 (0)	0.66 (0)	-0.73 (0)
576km^2 (6km)	-0.4 (0)	0.7 (0)	-0.69 (0)
784km^2 (7km)	-0.33 (0)	0.69 (0)	-0.73 (0)
1024km^2 (8km)	-0.36 (0)	0.65 (0)	-0.52 (0)
1296km^2 (9km)	-0.31 (0)	0.62 (0)	-0.51 (0)
1600km^2 (10km)	-0.42 (0)	0.79 (0)	-0.57 (0)
1936km^2 (11km)	-0.41 (0)	0.72 (0)	-0.4 (0)
2304km^2 (12km)	-0.24 (0.03)	0.67 (0)	-0.55 (0)
2704km^2 (13km)	-0.12 (0.39)	0.66 (0)	-0.67 (0)
3136km^2 (14km)	-0.29 (0.03)	0.77 (0)	-0.66 (0)
3600km^2 (15km)	0.18 (0.27)	0.4 (0.01)	-0.65 (0)

Table C.12: Correlation between the mean distance moved and the estimated value g_0, σ, and density, for different levels of survey areas when 25 cameras are used

Area (Spacing) 43cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
30km^2 (1km)	0.02 (0.72)	0.39 (0)	-0.53 (0)
120km^2 (2km)	-0.22 (0)	0.64 (0)	-0.72 (0)
270km^2 (3km)	-0.21 (0)	0.62 (0)	-0.72 (0)
480km^2 (4km)	-0.12 (0)	0.57 (0)	-0.65 (0)
750km^2 (5km)	-0.17 (0)	0.61 (0)	-0.63 (0)
1080km^2 (6km)	-0.2 (0)	0.59 (0)	-0.57 (0)
1470km^2 (7km)	-0.34 (0)	0.67 (0)	-0.52 (0)
1920km^2 (8km)	-0.31 (0)	0.67 (0)	-0.53 (0)
2430km^2 (9km)	-0.26 (0)	0.66 (0)	-0.57 (0)
3000km^2 (10km)	-0.3 (0)	0.71 (0)	-0.52 (0)
3630km^2 (11km)	-0.2 (0)	0.6 (0)	-0.52 (0)
4320km^2 (12km)	-0.14 (0.06)	0.67 (0)	-0.59 (0)
5070km^2 (13km)	-0.08 (0.34)	0.64 (0)	-0.64 (0)
5880km^2 (14km)	-0.07 (0.48)	0.69 (0)	-0.64 (0)
6750km^2 (15km)	-0.08 (0.41)	0.65 (0)	-0.53 (0)

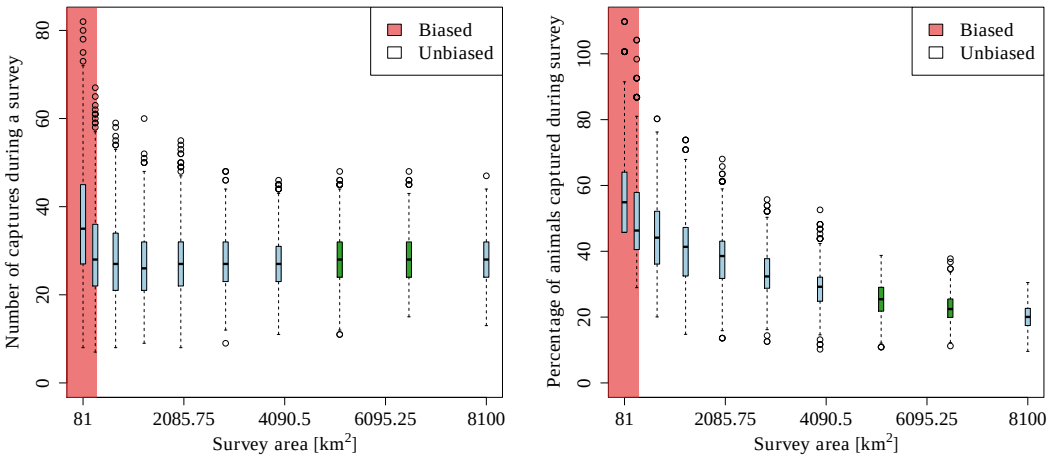
Table C.13: Correlation between the mean distance moved and the estimated value g_0, σ, and density, for different levels of survey areas when 42 cameras are used

Area (Spacing) 26cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
16km^2 (1km)	-0.09 (0.36)	0.34 (0)	-0.41 (0)
64km^2 (2km)	-0.28 (0)	0.64 (0)	-0.7 (0)
144km^2 (3km)	-0.49 (0)	0.72 (0)	-0.63 (0)
256km^2 (4km)	-0.58 (0)	0.78 (0)	-0.64 (0)
400km^2 (5km)	-0.63 (0)	0.81 (0)	-0.52 (0)
576km^2 (6km)	-0.68 (0)	0.86 (0)	-0.45 (0)
784km^2 (7km)	-0.67 (0)	0.89 (0)	-0.44 (0)
1024km^2 (8km)	-0.69 (0)	0.86 (0)	-0.13 (0.06)
1296km^2 (9km)	-0.66 (0)	0.82 (0)	-0.07 (0.38)
1600km^2 (10km)	-0.66 (0)	0.84 (0)	-0.09 (0.37)
1936km^2 (11km)	-0.64 (0)	0.76 (0)	0.17 (0.12)
2304km^2 (12km)	-0.62 (0)	0.76 (0)	-0.01 (0.95)
2704km^2 (13km)	-0.5 (0)	0.68 (0)	-0.12 (0.37)
3136km^2 (14km)	-0.49 (0)	0.6 (0)	-0.08 (0.55)
3600km^2 (15km)	-0.5 (0)	0.53 (0)	0.18 (0.27)

Table C.14: Correlation between the maximum distance moved and the estimated value g_0, σ, and density, for different levels of survey areas when 25 cameras are used

Area (Spacing) 43cams	G0 correlation (p-value)	SIGMA correlation (p-value)	DENSITY correlation (p-value)
30km^2 (1km)	0.07 (0.33)	0.24 (0)	-0.26 (0)
120km^2 (2km)	-0.26 (0)	0.63 (0)	-0.6 (0)
270km^2 (3km)	-0.4 (0)	0.72 (0)	-0.54 (0)
480km^2 (4km)	-0.46 (0)	0.79 (0)	-0.36 (0)
750km^2 (5km)	-0.49 (0)	0.8 (0)	-0.36 (0)
1080km^2 (6km)	-0.58 (0)	0.82 (0)	-0.2 (0)
1470km^2 (7km)	-0.65 (0)	0.84 (0)	-0.12 (0.01)
1920km^2 (8km)	-0.63 (0)	0.84 (0)	-0.13 (0.01)
2430km^2 (9km)	-0.63 (0)	0.84 (0)	-0.14 (0.01)
3000km^2 (10km)	-0.59 (0)	0.81 (0)	-0.01 (0.87)
3630km^2 (11km)	-0.6 (0)	0.77 (0)	-0.02 (0.73)
4320km^2 (12km)	-0.52 (0)	0.7 (0)	-0.05 (0.48)
5070km^2 (13km)	-0.46 (0)	0.7 (0)	-0.14 (0.08)
5880km^2 (14km)	-0.32 (0)	0.53 (0)	-0.03 (0.74)
6750km^2 (15km)	-0.38 (0)	0.59 (0)	-0.06 (0.54)

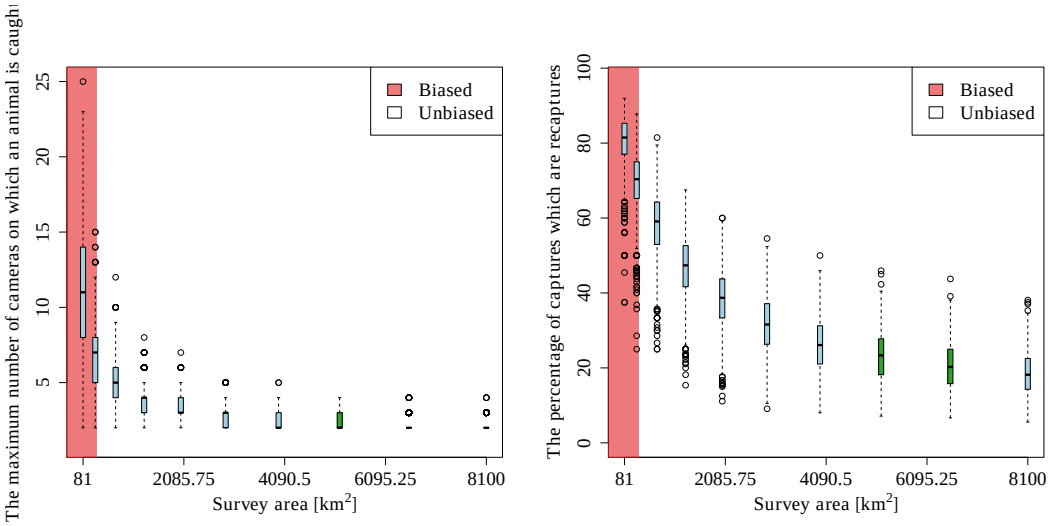
Table C.15: Correlation between the maximum distance moved and the estimated value g_0, σ, and density, for different levels of survey areas when 42 cameras are used



(a) Change in number of captures with change in survey design

(b) Change in percentage of animals captured with change in survey design

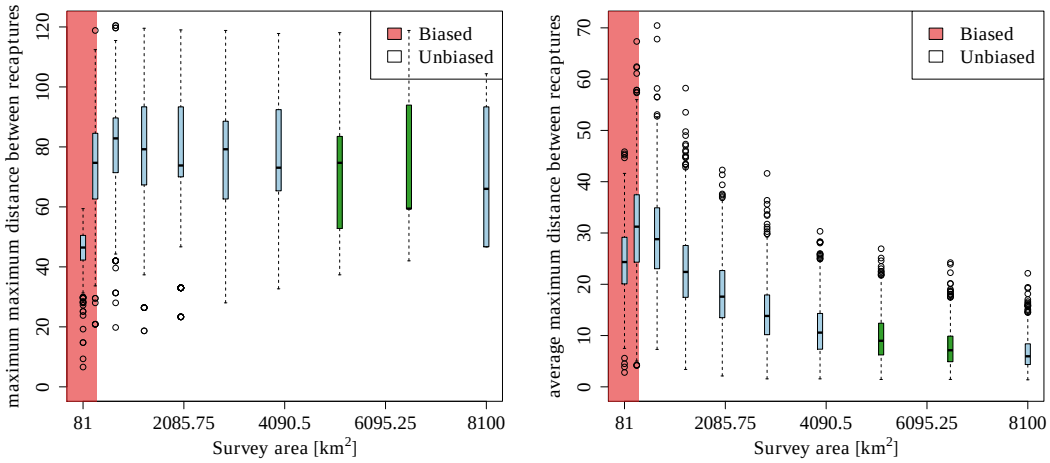
Figure C.5: The change in collected data when 100 cameras were used in different survey designs, with intertrap distances ranging from 1 km to 15 km. Where in plot a) the y-axis shows the number of captures, and in plot b) the y-axis shows the percentage of animals that were captured. Where based on the guidelines discussed in chapter 2, box plots in the red area should be biased due to small survey areas or wide inter trap distances, and where a green box plot shows that the median bias was not significantly different to zero, and a light blue box plot shows that the median density bias was significantly different from zero.



(a) Change in the maximum number of cameras an animal visits with variation in survey design

(b) Change in percentage of captures with variation in survey design

Figure C.6: The change in collected data when 100 cameras were used in different survey designs, with intertrap distances ranging from 1 km to 15 km. Where in plot a) the y-axis shows the maximum number of cameras any one animal visits, and in plot b) the y-axis shows the percentage of captures that were recaptures. Where based on the guidelines discussed in chapter 2, box plots in the red area should be biased due to small survey areas or wide inter trap distances, and where a green box plot shows that the median bias was not significantly different to zero, and a light blue box plot shows that the median density bias was significantly different from zero.



(a) Change in the maximum number of cameras an animal visits with variation in survey design

(b) Change in percentage of captures with variation in survey design

Figure C.7: The change in collected data when 100 cameras were used in different survey designs, with intertrap distances ranging from 1 km to 15 km. Where in plot a) the y-axis shows the maximum number of cameras any one animal visits, and in plot b) the y-axis shows the percentage of captures that were recaptures. Where based on the guidelines discussed in chapter 2, box plots in the red area should be biased due to small survey areas or wide inter trap distances, and where a green box plot shows that the median bias was not significantly different to zero, and a light blue box plot shows that the median density bias was significantly different from zero.

Appendix D

Chapter 4

The equation for $\bar{p}$ has been newly derived for each submodel in the gREM, except for the gas model and REM which have been calculated previously. However, many models, although derived separately, have the same expression for $\bar{p}$. Figure D.1 shows the expression for $\bar{p}$ in each case. The general equation for density, 5.1, is used with the correct value of $\bar{p}$ substituted. It can be seen that all adjacent expressions in Figure D.1 are equal when expressions for the boundaries between them are substituted in.

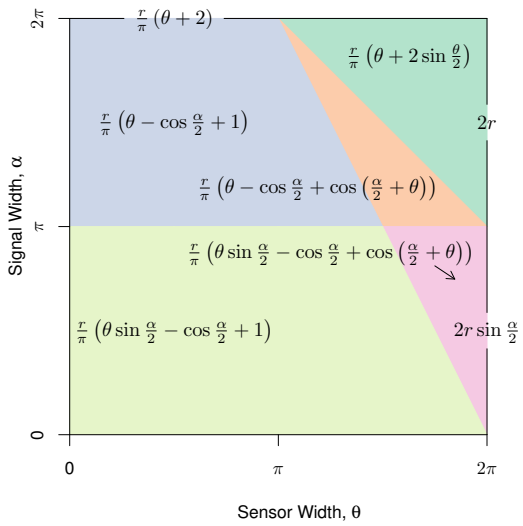


Figure D.1: Expressions for the average profile width, $\bar{p}$, given a range of sensor and signal widths. Despite independent derivation within each block, many models result in the same expression. These are collected together and presented as one block of colour. Expressions on the edge of the plot are for submodels with $\alpha, \theta = 2\pi$.

Symbol	Description	Units
θ	Sensor width	rad
α	Animal signal width	rad
x_i	Focal angle, $i \in \{1,2,3,4\}$	rad
r	Detection distance	m
$\bar{p}$	Average profile width	m
p	A specific profile width	m
v	Velocity	$\mathrm{m\,s^{-1}}$
t	Time	s
z	Number of detections	-
D	Animal density	$\mathrm{m^{-2}}$
T	Step length	s
N	Number of steps per simulation	-
d	Distance moved in a time step	m
S	Probability of remaining stationary	-
A	Maximum turning angle	rad

Table D.1: List of symbols used to describe the gREM and simulations. '-' means the quantity has no units.